ASPECTS OF THE BIOLOGY AND LOCAL DISTRIBUTION OF SEA STARS INHABITING A SLOPED, ROCKY BOTTOM IN LOGY BAY, NEWFOUNDLAND

IAIN PAUL EMERSON

ASPECTS OF THE BIOLOGY AND LOCAL DISTRIBUTION OF SEA STARS INHABITING A SLOPED, ROCKY BOTTOM IN LOGY BAY, NEWFOUNDLAND

by

© Ian Paul Emerson, B.Sc.

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of the requirements for the degree of
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Marine Sciences Research Laboratory
Department of Biology
Memorial University of Newfoundland

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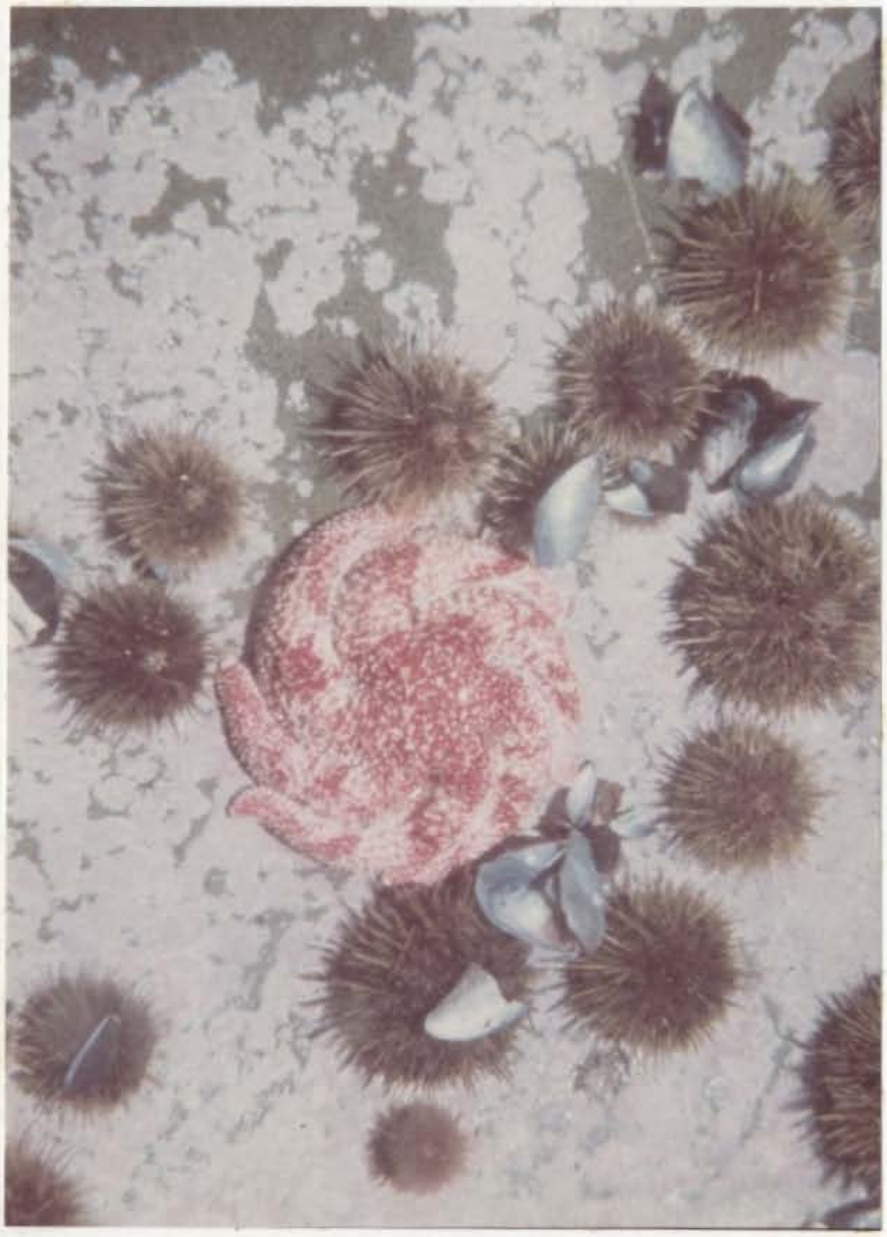
Frontispiece. A female Leptasterias polaris (Muller and Troschel, 1842) in a brooding position.



Abstract

The spatial and temporal distribution of five species of asteroids were examined over a one year sampling programme by means of a series of photographs taken weekly along a set transect line extending perpendicularly down a sloped sublittoral rocky bottom, in Logy Bay, Newfoundland. Estimates of the abundance and distribution of three species of asteroids inhabiting a more gently sloped sublittoral plateau surmounting this underwater cliff were also determined using a variety of quantitative and qualitative sampling techniques.

The results of systematic studies of selected physical, chemical, and biological characteristics of these habitats are presented. Such characteristics include depth, slope, relative irradiance, water temperature, dissolved oxygen concentration, conductivity, and predator and prey abundance and distribution.

Specific studies relating to the interaction of sea stars with their environment (i.e. feeding, light preference, pull capacity, and interspecific and intraspecific behaviour), undertaken to elucidate factors affecting sea star distribution, are also presented.

A presentation of the effects of other specific biological activities on local distribution patterns, such as migration and movement, reproduction and growth is also given.

In the general discussion, a hypothetical model for considering interactions between a species and its environment that affect population dynamics and local distribution is presented. The model is then utilized in an analysis of locally observed asteroid distribution patterns in the study area. From this analysis it is concluded that the distribution

or occurrence of water disturbance, prey, predators, and competitors are the major factors affecting the abundance-distribution patterns of the sea stars in the study area. A wider range of interactions between a given species and its environment may be of secondary importance in this relationship.

"... one is impressed not with the knowledge gained, but rather with the numerous questions still to be answered."

Feder and Christensen

'Aspects of Asteroid Biology',

in "Physiology of Echinodermata",

edited by R.A. Boolootian, 1966.

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GENERAL INTRODUCTION

Factors affecting the local distribution of sea stars has long been a topic of interest to asteroid biologists, and yet it remains one of the most poorly understood aspects of sea star biology. Many authors have commented on this area but have failed to come to grips with the multiplicity of factors involved in these complex relationships.

Mead (1900) was probably the first author to attempt an explanation of the lack of uniformity in the distribution of sea stars at a specific location. He established that two closely related species, Asterias vulgaris (Verrill) and A.forbesi (Desor) had dissimilar distributions resulting possibly from "natural barriers" within the environment such as depth, density of water, and barren bottom (i.e. lack of food).

Huntsman (1918) discovered that A.vulgaris was absent from sloped areas. This observation he equated to fluctuating temperatures on the slope.

In a major research programme to control the oyster predator, A.forbesi, Galtsoff and Loosanoff (1939) undertook an extensive study of the distribution of this species in the waters off New England. They ruled out temperature, salinity, and substrate, as being important factors controlling its distribution and related large concentrations of sea stars to the presence of molluscs.

Smith (1940), conversely, in a similar study on A.vulgaris in the waters around Prince Edward Island, established that low salinity

and high temperature could be limiting factors, producing natural mortality, but also related a high density of sea stars to a high density of prey.

Recently, other authors have also related the distribution of asteroid species to prey. Hancock (1958) gives evidence that the distribution of A.rubens (L.), is primarily affected by the distribution of Crepidula fornicata (L.), and Larsson (1968) reiterates this conclusion but refers to Mytilus edulis (L.) as the main prey of this asteroid.

The effects of temperature and salinity were examined with respect to distribution by Ursin (1960), studying the echinoderms of the North Sea. He found that temperature was unimportant in limiting their distribution, with the exception of one species, Astropecten irregularis (Pennant). Of interest in this study, however, was his conclusion regarding the genus Henricia (Gray). Not finding that temperature and salinity per se accounted for its distribution, he related their distribution to the presence of Sagitta elegans (Verrill) water, i.e. water rich in nutrients, necessary to satisfy their mode of suspension feeding (Rasmussen, 1965).

A number of researchers have considered the distribution of asteroids in conditions obviously limited by salinity such as in the Baltic Sea (Meyer, 1935; Brattstrom, 1941; Kowalski, 1955; Schlieper, 1956); in brackish water (Brattstrom, 1941; Ursin, 1960); and in sudden fresh water runoff situations (Crozier, 1920; MacGinitie, 1939; Loosanoff and Engle, 1940; Loosanoff, 1945; Smith, 1940).

Verrill (1914) was one of the first to address the problem of seasonal fluctuation in asteroid populations. His conclusions that

sea stars migrated into shallow water for feeding in the fall and returned to deeper water during the winter period to escape cold surface temperatures, were, however, refuted by Galtsoff and Loosanoff (1939).

Similar annual migrations by other sea star species appear to be well documented. O'Donoghue (1924) studied the summer migration of sea stars of the littoral zone at Departure Bay, British Columbia. He noted that exposure to air during periods of high temperature and direct sunlight was the most likely factor controlling their migration to deep water. Hewatt (1937) found that Leptasterias aequalis (Stimpson) migrated to deeper water for reasons associated with reproduction.

The problem of exposure to air has been discussed by a variety of authors (summarized by Feder and Christensen, 1966). Recently, Landenberger (1969) noted that the differences in ability of three species of the genus Pisaster (Brandt) to cope with exposure to air has resulted in differences in the distribution of these species.

The question of substrate as a factor affecting distribution has been dealt with most adequately by Grainger (1966) in his discussion of distribution of sea stars in the Canadian Arctic. He showed that species can be divided into three groups depending upon the type of substrate on which they are found. His first and third groups comprise species that are found only on soft and hard bottoms, respectively, and his second group includes those species which are found on a wide range of bottom types.

Hence, from previous studies, we see that sea star distribution may be controlled by a wide range of parameters. Several criticisms, however, can be directed at the scope of many of these studies (but

notably not all). Usually, distribution has been considered in terms of one or two factors which absolutely exclude a particular species from a specific habitat. As yet we do not have a complete appreciation of why abundances of a particular species vary within a particular locale, or why the abundance-distribution patterns of different species vary. Most of these studies have dealt with the problem of why a species is present or absent in a collected sample, and not on observations made within the animals' environment. Many types of habitats, particularly rock bottoms, have received little attention, and many species have yet to be discussed. The majority of authors have failed to study how a species interacts with its environment to produce its individual abundance-distribution patterns.

During the summer of 1968, while a summer student working at the Marine Sciences Research Laboratory for Dr. J. Berger of the University of Toronto, I became intrigued with this problem. Following conversations with Dean F.A. Aldrich, then Director of the M.S.R.L., and with divers who were employed to collect specimens for the M.S.R.L., I became aware that the various sea star species found in Logy Bay had different local distribution patterns. Owing to my interest in this topic, I was encouraged by Dean Aldrich to undertake a Master's programme to attempt to establish what factors were responsible for causing these apparent species differences in distribution.

After completing an extensive literature survey, I was amazed to discover that no information existed on the biology of sea stars in Newfoundland waters, that little information was available on the physical, chemical, and biological characteristics of their habitat,

and that little, if any, of the general asteroid literature could be directly applied to this topic. Hence, I set out to study the spatial and temporal distribution of the various sea stars species, the biological characteristics which may affect their distribution, and the environmental parameters affecting this relationship.

A. Study Area Sea Stars:

Systematics, Description, and Geographic Distribution

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A. Study Area Sea Stars: Systematics, Description, and Geographic Distribution

Seven species of sea stars inhabit the study area, five of which could be easily identified to species, whereas the remaining two species presented taxonomic difficulties. The following section lists the description, systematics, and geographic and bathymetric distributions of the five positively identified species. Brief notes on the unidentified species are included.

A-I Order Forcipulata

Family Asteriidae

Species Asterias vulgaris Verrill[1]

Synonomy:

"Asterias vulgaris Packard, 1863 (nomen nudum).

Asterias stimpsoni Verrill, 1866.

Asterias vulgaris Verrill, 1866.

Asterias pallida Perrier, 1875.

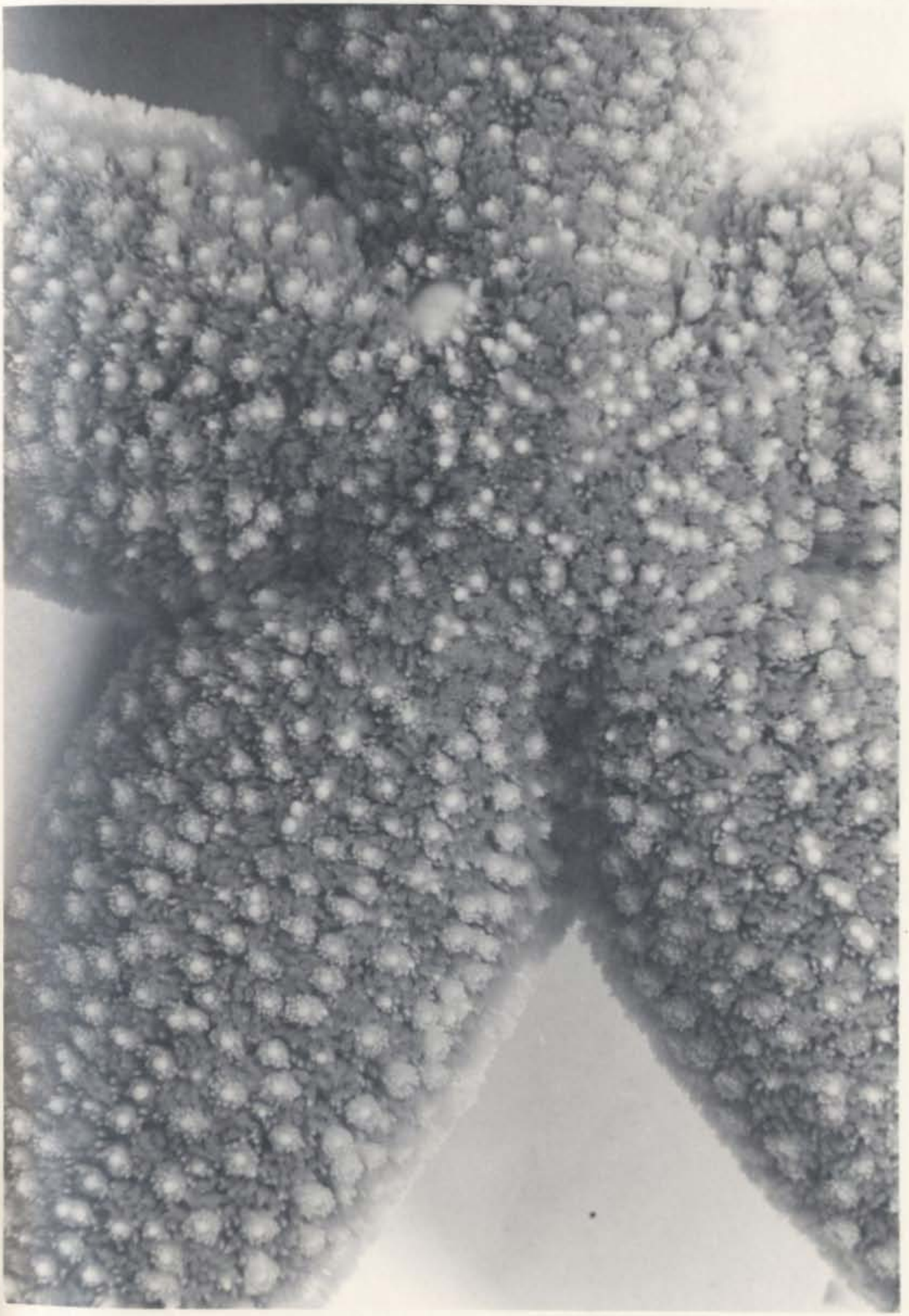
Asterias fabricii Perrier, 1875.

A-I.1 Description: (fig. 1)

Disc of moderate size, arms five, more flattened and pointed than in A.forbesii. Aboral surface a network of narrow barlike plates with

[1] Tortonese (1963, cited by Swan, 1966) states that "A.vulgaris is conspecific with A.rubens and not even separable on a subspecific basis." This species (A.rubens) is distributed from Senegal to Iceland and northern Norway, but not in the Mediterranean. It is also found in the south of the Barents Sea, almost as far as Svyatoi Nos in Kola Bay, and in the White Sea. Recently, it has been found off the coast of Greenland. Its bathymetric range is 0 to 400 meters. (D'yakonov, 1950).

Figure 1. Photograph of the aboral surface of Asterias vulgaris. Magnification 3 X. Refer to the text for description.



large meshes, making a fairly weak skeleton. Clearly perceptible row of median plates. All plates with one or more blunt spines with rough tips, encircled by a wreath of blunt pedicellariae. Large acute pedicellariae along sides of arms, rising directly from dermis. Inferomarginals with conspicuous series of long, truncate spines. Adambulacrals with one or two long, flattened spines. Rr=3:1. Color reddish brown, madreporite usually yellow." from Gray et al (1968).

A-I.2 Geographic and Bathymetric Range

The geographic range of A.vulgaris is from Labrador to Cape Hatteras, occupying a bathymetric range of 0 to 650 meters (Gray et al, 1968).

A-II Order Forcipulata

Family Asteriidae

Species Leptasterias polaris (Muller and Troschel)

Synonomy:

"Asteracanthion polaris Muller and Troschel, 1842.

A.polare Duncan and Sladen, 1881.

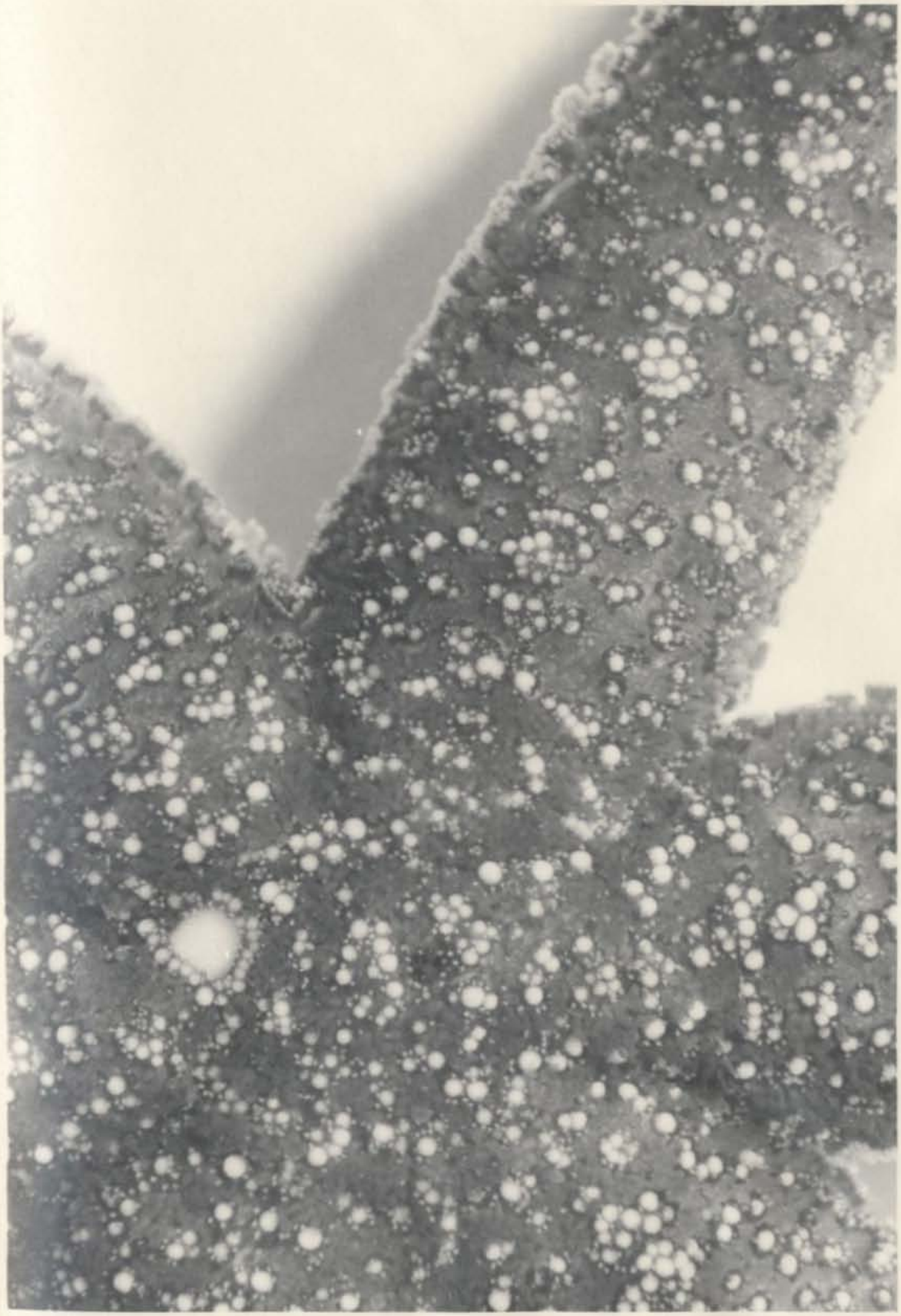
Leptasterias polaris Fisher, 1930.

L.polaris acervata Fisher, 1930.

A-II.1 Description (fig. 2)

Usually 6 rays. R:r at least 3.5:1 to 6.3:1. Aboral surface a strong, fairly close-meshed network, with spines which vary greatly in size, shape, and arrangement in the different reported subspecific forms. Aboral spines, generally of stout construction, frequently with bulbous ends (although in some they may be relatively longer and

Figure 2. Photograph of the aboral surface of Leptasterias polaris. Magnification 3 X. Refer to the text for description.



cylindrical to the tip), and often in groups of several small spines surrounding a larger central one, or less frequently as solitary spines of varying density. Not infrequently aboral spine groups with some semblance of regularity along the carinal rows at least, and sometimes additionally in one dorsolateral row longitudinally along either side of the carinals; elsewhere usually scattered. Marginal and ventrolateral spines cylindrical and longer and relatively more slender than the aborals, in 3 or 4 conspicuously regular longitudinal rows along much of the length of the rays. Adambulacral spines, cylindrical, relatively more slender and shorter than the lateral spines, frequently as 2, less often as 1 per plate. Sometimes long consecutive series of 2-per-plate pairs of spines alternate regularly in position giving superficially the impression of 4 rows of spines along each side of the groove." from Grainger (1966).

A-II.2 Geographic and Bathymetric Range

The geographic range of this species is from the Bering Sea eastward to East Greenland and southward in the west Atlantic to New England, occupying a depth range of 0 to 110 meters (Grainger, 1966).

A-III Order Spinulosa

Family Solasteridae

Species Solaster endeca (L).

Synonomy:

" Solaster endeca Duncan and Sladen, 1881.

S.endeca Danielssen and Koren, 1884.

S.endeca Doderlein, 1900.

S.endeca Fisher, 1911.

S.endeca Mortensen, 1927.

A-III.1 Description (fig. 3)

Rays 7-13, most frequently 9 or 10. R:r about 2.3:1 to 3.3:1. Aboral paxillae small, higher than broad, more or less scattered, with from at least 4 to about 15 spines. Inframarginal plates larger than supramarginals, transversely elongate. Supramarginal paxillae only a little larger than adjacent dorsolateral paxillae, but clearly distinguishable from them. Inner adambulacral spines set in the groove, from 1 or 2 to 4 in number, much shorter and less conspicuous than the larger outer adambulacral spines. These, in transversely placed rows, vary from about 3 to 7 or 8 in number, the innermost spines the longest and stoutest, the outermost the smallest. Tube-feet in 2 rows. Oral interradial spaces with paxillae." from Grainger (1966).

A-III.2 Geographic and Bathymetric Range

This species ranges from the eastern arctic to the Kara Sea, south to New England in the western Atlantic, and south to the British Isles in the eastern Atlantic. In the eastern Pacific, it ranges from Point Barrow, Alaska, south to Vancouver Island. Depth range in northern Canada is 18 to 118 meters (Grainger, 1966).

A-IV Order Spinulosa

Family Solasteridae

Species Crossaster papposus[1] (L.)

---

[1] Many authors do not differentiate between the genera, Crossaster and Solaster; however, convincing arguments by D'yakonov (1950) based on differences outlined by Fisher justify the usage of the genus Crossaster. Recently, many authors have used Crossaster papposus as the name of this species (eg. Castilla and Crisp, 1970; Mauzey et al, 1968; and Feder and Christensen, 1966).

Figure 3. Photograph of the aboral surface of Solaster endeca. Magnification 3X. Refer to the text for description.

Synonomy:

"Crossaster papposus Duncan and Sladen, 1881

Solaster papposus Doderlein, 1900.

S.papposus Grieg, 1907.

S.papposus Fisher, 1911.

S.papposus Mortensen, 1927.

S.papposus Heding, 1935.

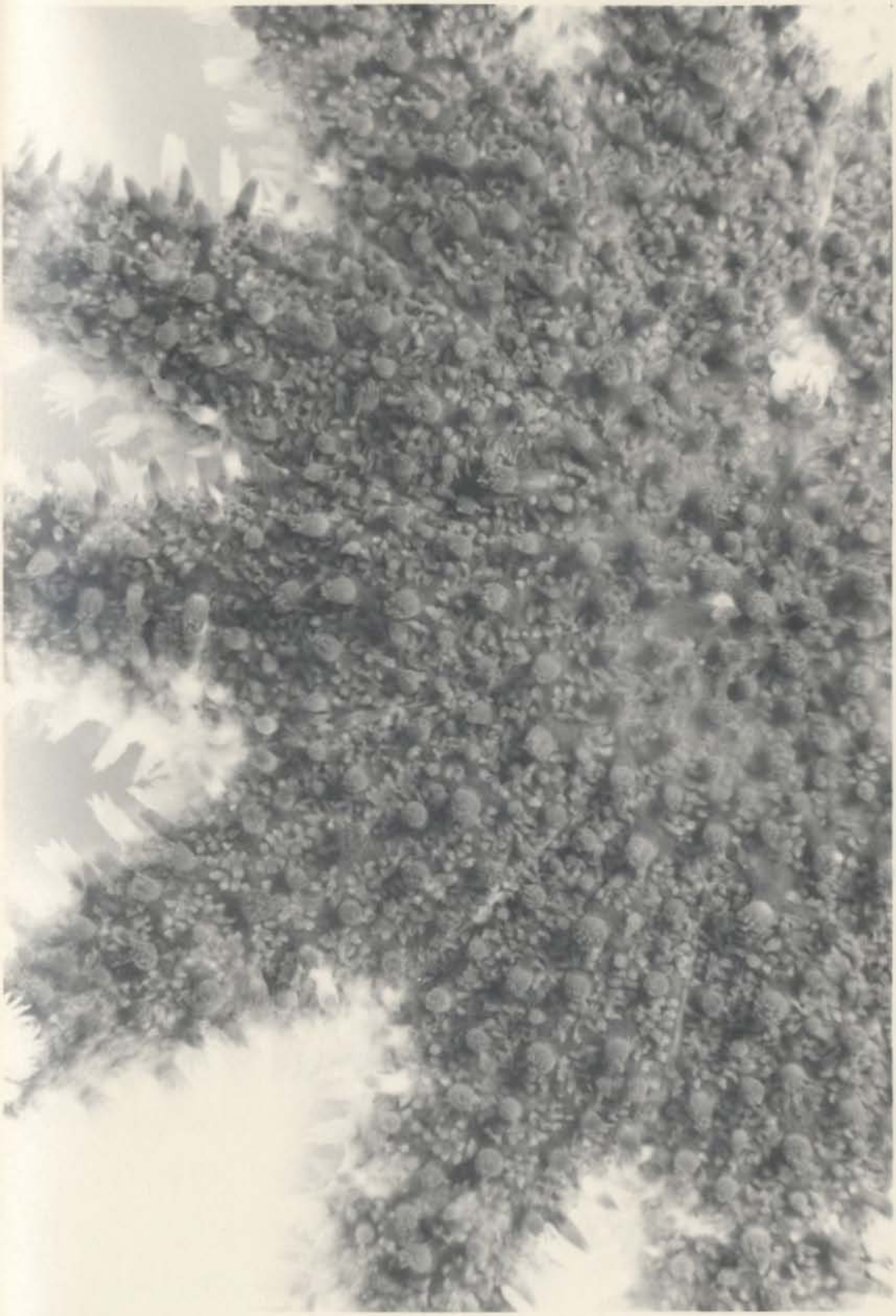
A-IV.1 Description (fig. 4)

Eight to 16 rays, most frequently 10-12, R:r about 1.7:1 to 2.7:1. Aboral skeleton an open reticulated network, with up to 50 spines per paxilla. Inframarginal plates with a single conspicuous row of paxillae; supramarginals almost indistinguishable from aboral paxillae. Inner adambulacral spines arranged parallel to the groove, numbering usually 3-4, occasionally 2 to at least 7; outer adambulacral spines in rows at right angles to the groove numbering usually about 5-7, rarely 3-9. Oral plates with 6-11 marginal spines. Tube-feet in 2 rows." from Grainger (1966).

A-IV.2 Geographic and Bathymetric Range

C.papposus is an arctic boreal species extending southward to 40° N (approximately New Jersey) in the western Atlantic, and to Great Britain in the eastern Atlantic. In the Pacific, it extends to Vancouver Island and Japan on the eastern and western sides, respectively. It has an extremely wide bathymetric range of 0 to 1200 meters (D'yakanov, 1950).

Figure 4. Photograph of the aboral surface of Crossaster papposus. Magnification 2 X. Refer to the text for description.



A-V Order Spinulosa

Family Echinasteridae

Species Henricia eschrichti[1] (Muller and Troschel)

Synonomy:

"Echinaster eschrichtii Muller and Troschel, 1842.

Cribrella oculata Duncan and Sladen, 1881.

Henricia eschrichtii eschrichtii Heding, 1935.

Henricia eschrichtii eschrichtii Grainger, 1955.

A-V.1 Description (fig. 5)

Five rays, R:r about 3:1 to 4:1. Aboral skeleton irregularly and closely reticulated, dorsolateral, marginal and oral surface skeleton fairly regularly imbricated, with papular areas much narrower than plates. Carinal plates not readily distinguishable. Aboral paxillae with about 4-40 fairly small spines with usually 3 or 4 lateral ridges extending beyond the tip as a crown of 3 or 4 diverging points. Marginal plates large, conspicuous, in even imbricated rows and in close contact with adjacent rows. Adambulacral plates with usually 2 (sometimes 3) transverse rows of about 8-18 spines, the largest near the groove. Tube-feet in 2 rows." from Grainger (1966).

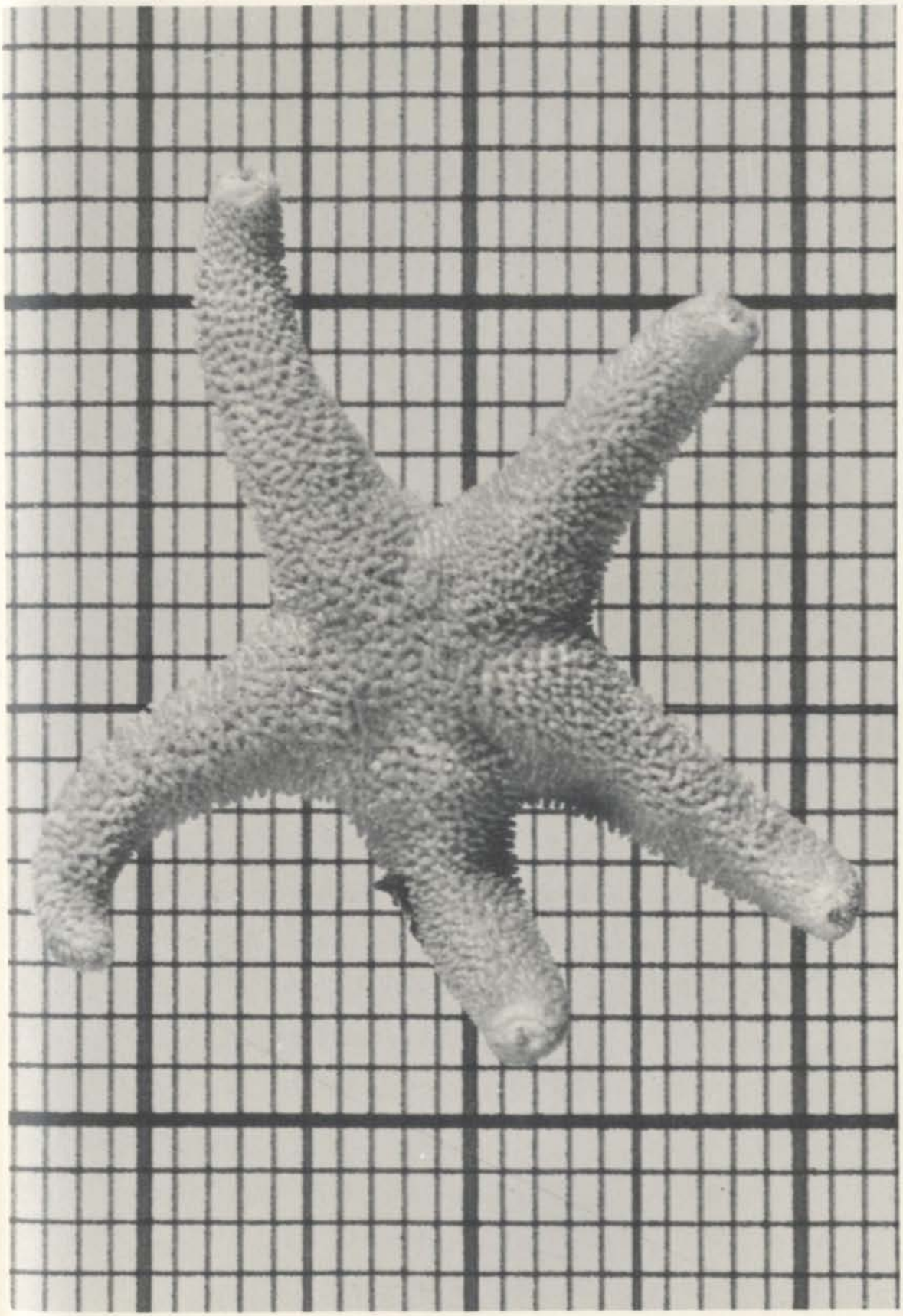
A-V.2 Geographic and Bathymetric Range

Since much confusion has existed with respect to the identification of this species, its distribution is difficult to determine. Grainger (1966) defined its North American distribution as being from Newfoundland to Baffin Island, and having a depth range of 14 (sic) to 148 meters.

---

[1] Since difficulties in identification of this species exist, specimens were sent to Grainger who confirmed my identification.

Figure 5. Photograph of the aboral surface of Henricia eschrichti. Magnification 5 X. Refer to the text for description.



A-VI. Unidentified Species

Of the two unidentified species, one is most definitely a species of the genus Henricia (fig. 6). Since members of this genus have proven to be "chronic sources of trouble to students of the group in northern waters" (Grainger, 1966), an intensive effort to identify this species was undertaken. It was felt that this species most closely resembled H.scabrior (Mikhailovskii), but demonstrated several characteristics which did not agree with the description by Grainger (1966) for this species. After examining several of these specimens, Dr. Grainger (personal communication) commented:

> "Your H.scabrior I must question, although I cannot give it another name. Either it is something not yet named or H.scabrior has wider structural limits than I once thought."

Since identification of this species is unclear, it is referred to as Henricia sp. throughout this thesis.

A similar situation existed for the other unidentified species (fig. 7). Based on a number of taxonomic characteristics, it should be assigned to the genus Leptasterias; however, positive species identification could not be made.[1] Since specimens of this species closely resembled juvenile Asterias vulgaris[2], both observations of this species and of juvenile A.vulgaris are excluded from this thesis to avoid confusion.

---

[1] Specimens of this species were also examined by Dr. Grainger and he too was unable to positively identify them.

[2] Underwater observations of this species brooding eggs in a manner similar to L.hexactis (Stimpson) (Chia, 1966), demonstrated that these specimens were not variant of A.vulgaris, a non-brooding species.

Figure 6. Photograph of the aboral surface of Henricia sp. Magnification 5X.

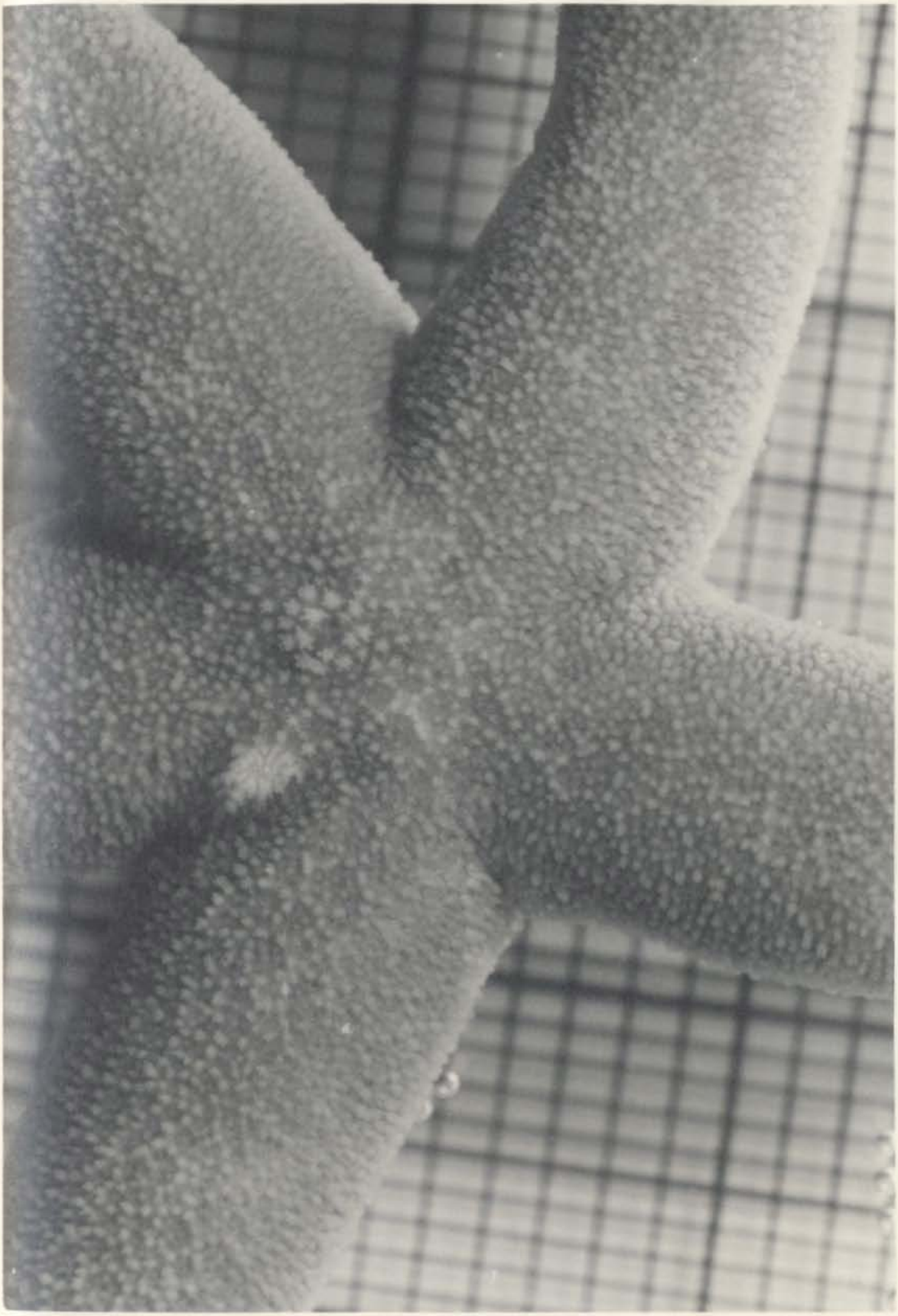


Figure 7. Photograph of the aboral surface of Leptasterias sp. Magnification 5X.

B. Study Area

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B. Study Area

B-I. Introduction

Selection of a study site was governed by three major criteria which were necessary in order to carry out this study.

1. A habitat was required which possessed a large depth gradient so that the distribution of asteroids could be considered over a range of physical, chemical, and biological parameters.
2. A high diversity of asteroid species was required for inter-specific comparison.
3. In order to eliminate problems of transportation of equipment and personnel, a close proximity to the facilities of the M.S.R.L. was required.

An ideal location according to these criteria was found at the head of Logy Bay, a bay facing northeasterly into the North Atlantic. The geographic centre of this study area had coordinates of 52^{o} 40' 54" W longitude, and 47^{o} 37' 37" N. latitude.

Boundaries of the study area (fig. 8) were determined such that a uniform substrate of red conglomerate bedrock characterized all portions of the study area. Based on topographic features the study area was divided into two major sections:

1. A shallow water plateau, roughly rectangular in shape, which extended seawards from Mad Rock 15-20 meters having a width of 20-30 meters was named the MAL zone after its three major benthic components, Mytilus edulis, Alaria esculenta (L) and Laminaria digitata (Huds.).

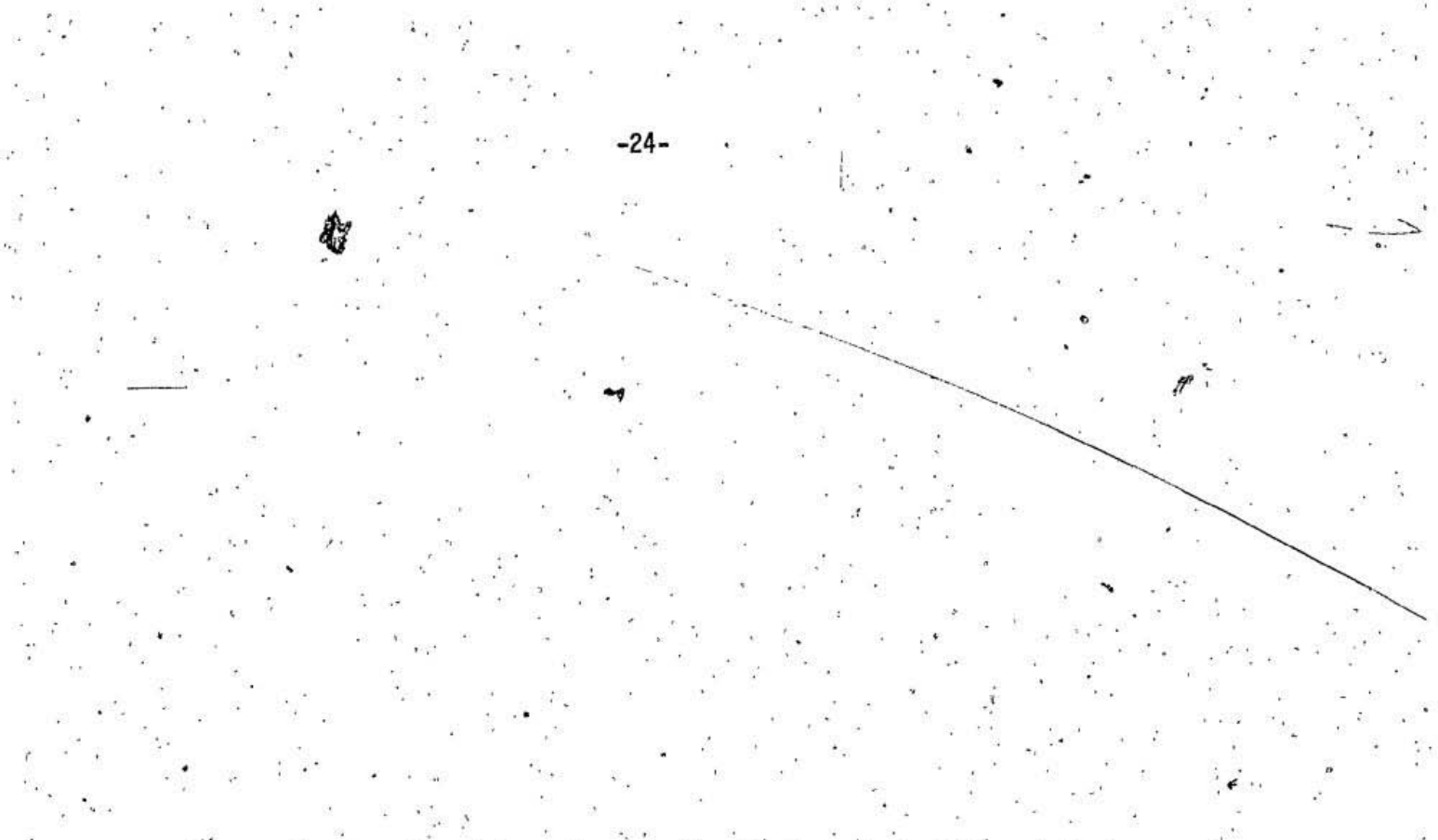
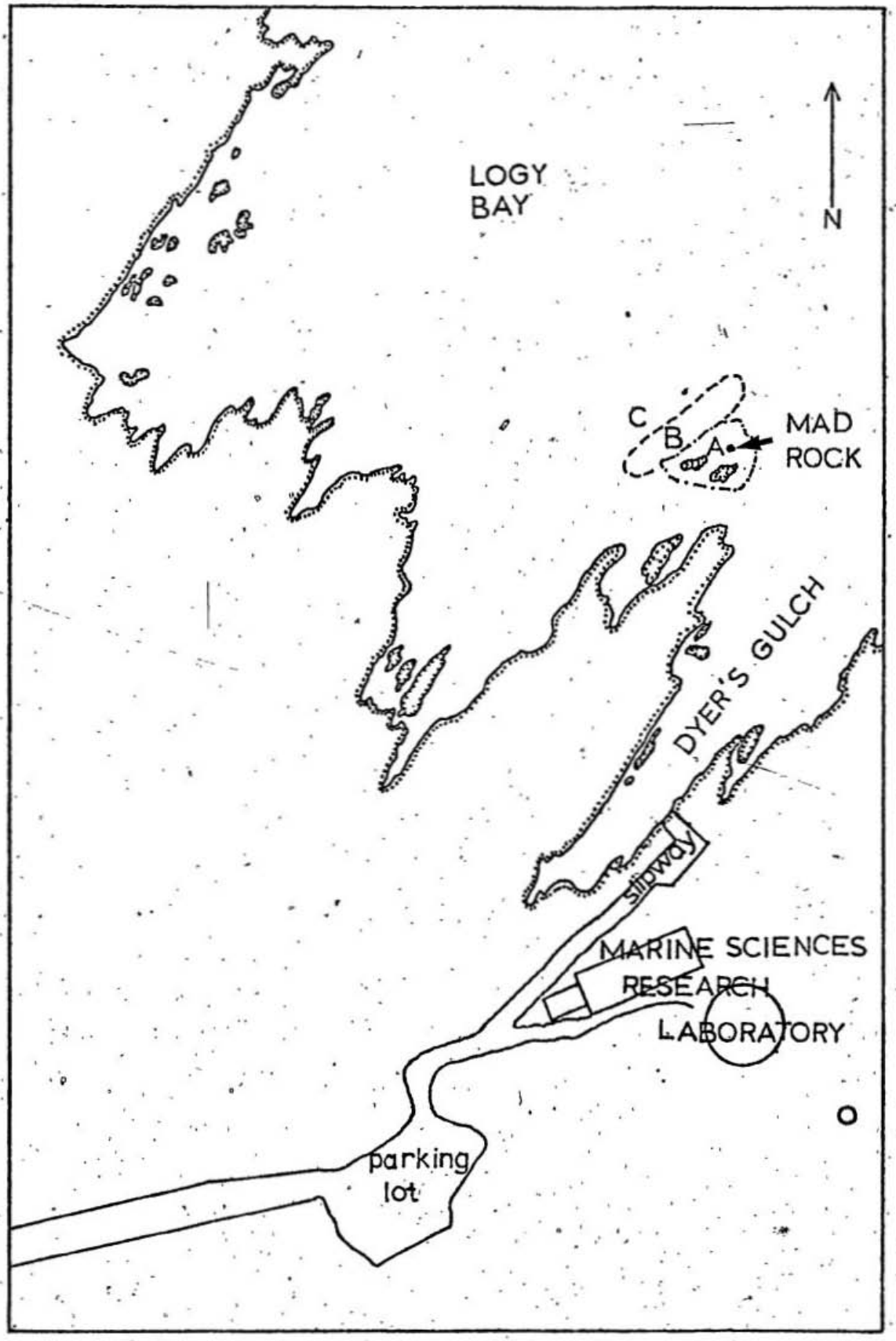


Figure 8. Drawing of Logy Bay showing the location of the study area.

A - MAL zone

B - Cliff area

C - Sand bottom


LOGY
BAY
N
C
B
A
MAD
ROCK
DYER'S GULCH
slipway
MARINE SCIENCES
RESEARCH
LABORATORY
parking
lot

2. A sloped area of bottom extending from the edge of the plateau at approximately 7 meters to an almost level sand bottom at 31 meters. Since no benthic components were dominant over the entire range of the slope, this area was named the Cliff Area after its dominant topographic feature.

B-II Topography

B-II.1 Materials and Methods

B-II.1 (i). Transect Line (TL)

In order that a point of reference existed for the various diving surveys undertaken throughout the course of the field study[1], a transect line was positioned in the cliff area[2].

---

[1] Note the importance of the TL is not restricted to its usage for merely surveying the topography of the cliff area but as a key reference point for other surveys administered in the cliff area including surveys of biota, and asteroid distribution.

[2] The TL was not extended into the MAL zone because of the high water disturbance, periodically characterizing this zone, which would have dislodged it.

The TL was a ¼" braided polypropylene rope which was held secure to the sand bottom by means of a large burlap bag filled with sand. To ensure that the rope did not move on the rocky slope, the TL was affixed to chrome steel pitons[1] (Hiatt PN7) which were driven into cracks on the rocky slope. In total length, the TL measured 36 meters and extended from a depth of approximately 9 meter to a depth of 31 meters (the horizontally flat sand bottom). The TL was aligned so that it ran down the gradient, parallel to the incline. At intervals of 1.5 meters, numbered laminated plastic cards (2" X 2") were attached to the TL by means of short lengths of nylon cord. In order to maintain the nylon cord at a fixed position, a small quantity of "Sea Goin" poxy putty was placed at its intersection with the TL. Thus when completed, the TL consisted of twenty-four 1.5 meter segments (called transect line quadrats, TLQ's), numbering from 1 to 24, increasing numerically from shallow to deep water.

---

[1] Since the untreated pitons were found to corrode in sea water, they were sand blasted and coated with carbo-zinc paint.

B-II.1 (ii). Depth

Since an annual tidal height range of 5.2 feet[1] existed in Logy Bay, the top of Mad Rock[2] was selected as the surface level. Measurements of depth were marked on the TL at depths of 10, 15, 20, 25 and 30 meters on July 6, 1970, a day when the surface of the water was flat calm. The tidal height at St. John's at the time the measurements were taken was 1.2 feet[3]. A measuring line was attached to a surface float and marked at one meter intervals with tape, and at 5 meter depth-intervals with a tied loop.

To determine the position for each 5 meter depth marking, a hook attached to a diver's lead weight was hung from the required loop. A piece of string was tied around the TL at the position where the lead weight just touched the bottom when the rope was taut and perpendicular to the surface. Each 5 meter depth mark position was recorded with respect to the TLQ numbered tags. The depth of the sand bottom was measured from the taped one meter intervals with the weight at the 30 meter loop. This value was later verified by use of a sounding line from a surface vessel.

B-II.1 (iii). Slope

To accurately determine the angle of inclination of the irregularly sloped study area, measurements of both the length and the slope of every differently sloped bottom segment had to be

---

[1] Canadian Tide and Current Tables, Vol. 1, The Atlantic Coast and Bay of Fundy: Canadian Hydrographic Service, 1970.

[2] Figure 8 shows the location of Mad Rock, near the upper end of the TL. Generally, it is exposed at low tide and covered at high tide (under calm water conditions).

[3] As in [1].

taken. With the 'clinometer' (fig. 9) held parallel and adjacent to the TL, the differently sloped regions were measured and recorded with respect to the TLQ numbered tags. Fig. 10 shows the stepwise procedure for measuring the irregular slope at TLQ 3. Clinometer readings (x), because of the position of the protractor, had to be converted to angle of inclination (θ) by the formula,

$\theta = 90^{o} - X$.

Figure 9. Diagram of clinometer.

a - protractor

b - plumb line

c - scale marked every 10 cm on dexion frame

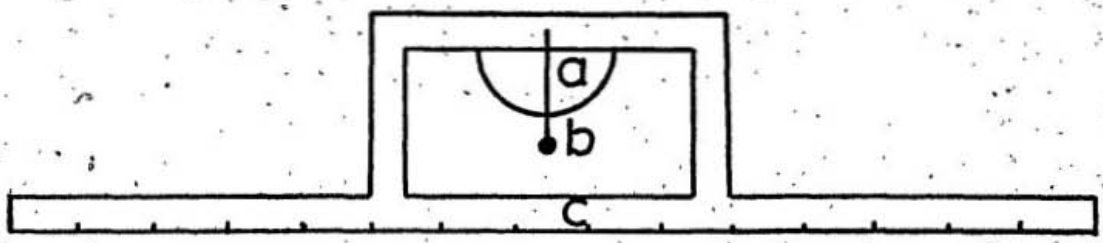
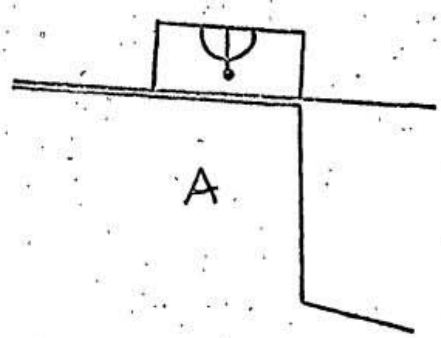
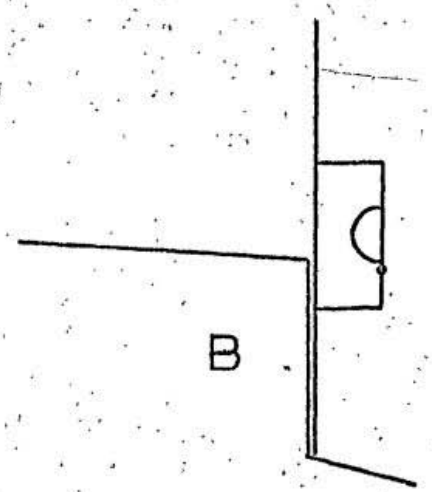
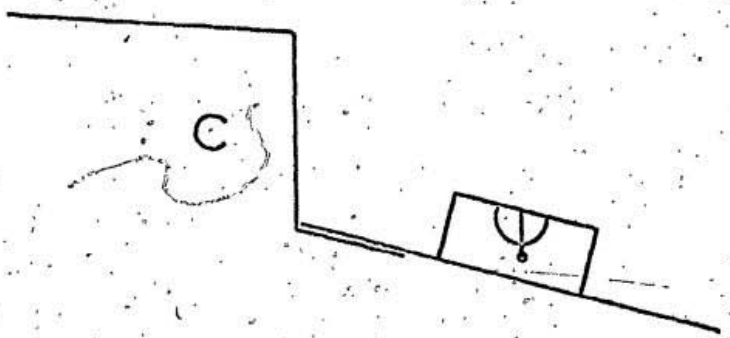

a
b
c

Figure 10. Diagrammatic representation of the stepwise procedure for determining the slope of an irregular bottom (TLQ 3).

The clinometer was positioned such that one end was flush with the numbered tag at TLQ 3 (A), and the distance (to the nearest 10 cm) of uniform slope was measured (here, 0.8 meters). Angle as measured by the clinometer (86^{o}) was recorded. To determine the angle of inclination (θ), angle (x) was subtracted from 90^{o}, i.e. $\theta = 90 - x$. B shows the measurement of the next slope (i.e. the distance from the last measurement to the end of the next uniform segment) and clinometer reading. Values were 0.7 meters and 0^{o} (x) or $\theta = 90^{o}$. Similarly, C shows measurement of the next slope from the last measurement to the TLQ 4 marker tag. Values were 0.3 meters and 77^{o} (x) or 13^{o} (θ).


A


B


C

B-II.2 Results and Discussion

B-II.2 (i). MAL Zone

Except for a few trenches displaying the northeast strike of the red conglomerate substrate, the MAL zone was almost uniformly flat, inclined at a slight angle so that depth of the plateau ranged from 3 meters at the base of Mad Rock to a maximum of 7 meters at its perimeter. It had an approximate area of 600 square meters.

B-II.2 (ii). Cliff Area

The sloping bottom of the cliff area was inclined at a mean angle of approximately 40^{o} to the horizontal; however, four major areas of differing slopes could be clearly recognized. These areas were designated B, C, D, E. From 8.7 meters depth to 12.7 meters, (area B), the red conglomerate substrate was gently sloping having an angle of inclination of 31^{o} to the horizontal. A similarly sloped area having an angle of inclination of 28^{o} was also present in the 20.5 to 24.0 meter depth range (area D). Between these gently sloping areas (i.e. 12.7 to 20.5 meter range), the bottom was more steeply inclined (54^{o}) (area C) and a similarly steeply sloped (51^{o}) area was present between 20.5 meters and the sand bottom at 31 meters (area E).

This pattern of alternating steeply sloping and gently sloping areas is shown in fig. 11, a cross-section of the cliff as measured along the TL. The slope and depth of each TLQ is shown in Table 1.

The width of the study area was determined by horizontal boundaries of each equally sloped region. The boundary of zones increased

Figure 11. Line drawing of the cliff profile showing the location of TLQ's. Vertical scale is in meters.

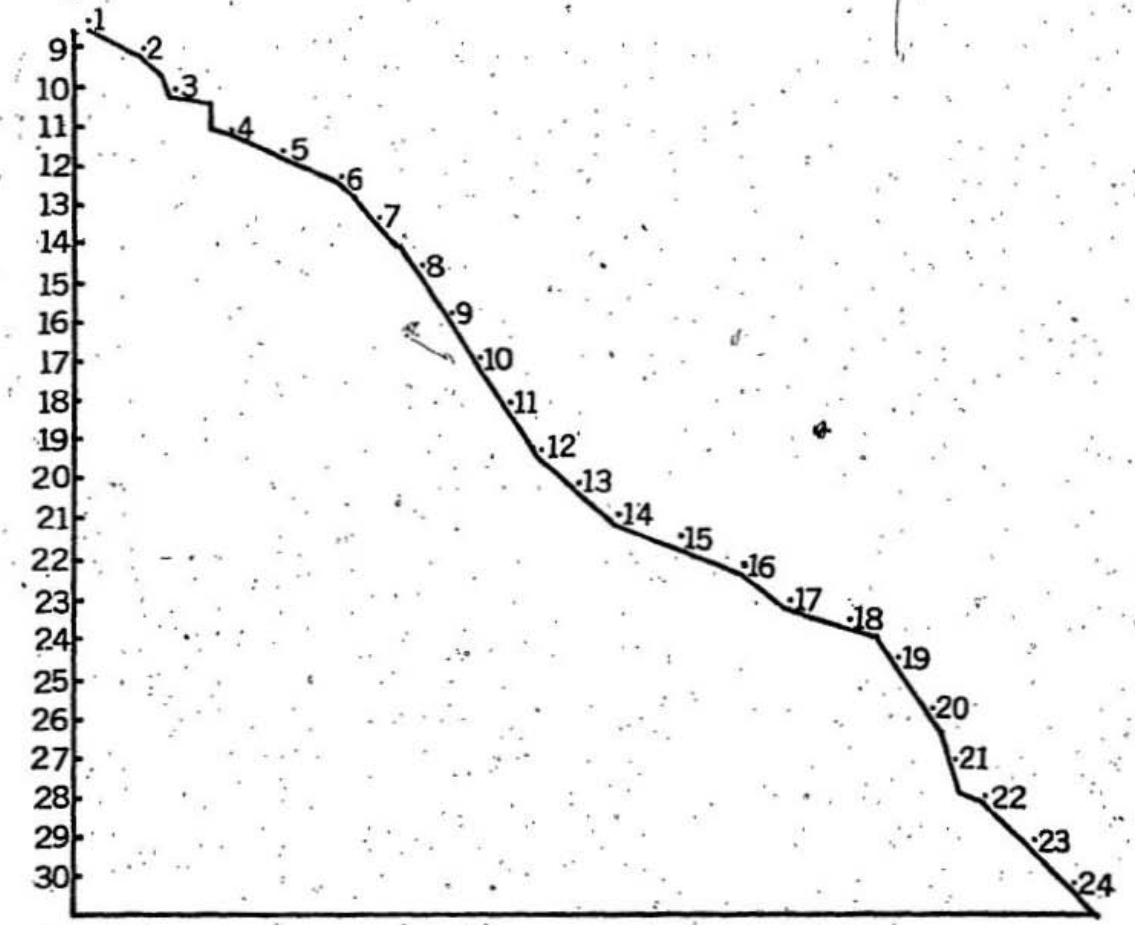

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Table 1. Depth-slope data for each TLQ.

Note:

1. Both slope and depth for each TLQ are determined from Figure 11.
2. Depth measurements were taken from the mid-point of each TLQ.
3. Slope was determined by joining adjacent TLQ numbers and measuring the slope of the resultant line.

TLQ Number	Depth (meters)	Slope (degrees)
1	9.0	24
2	9.8	47
3	10.5	36
4	11.5	22
5	12.1	24
6	12.8	43
7	13.9	52
8	15.2	56
9	16.4	56
10	17.6	56
11	18.9	56
12	20.0	36
13	20.9	41
14	21.6	19
15	22.1	20
16	22.8	37
17	23.5	17
18	23.9	35
19	25.2	55
20	26.3	62
21	27.8	50
22	28.7	44
23	29.7	42
24	30.8	48

with depth such that the horizontal boundaries of the study area formed a trapezoid configuration with the shallowest zone being approximately 25 meters in width and the deepest zone being 50 meters wide.

B-III. Physical and Chemical Description

B-III.1. Materials and Methods

Temperature, conductivity and oxygen measurements were taken on a weekly basis whenever possible. From August 6 to November 27, 1970, these parameters were measured either the day following the photographic series as described later, or, when this was not possible because of bad weather conditions, on the next possible day. Apart from two occasions in January 1971, the weekly series of measurements of physical parameters were discontinued until May 5, 1971 owing to bad weather conditions.[1] Throughout May, 1971, physical parameter data were again taken the day after the photographic series. During the months of June and July 1971, these parameters were measured on the same day as the photographic runs.

B-III.1 (i). Temperature, Depth and Conductivity (T.D.C.)

These parameters were measured using a Martex Model T.D.C. Metering system. This system consists of three major components: a transistorized battery-operated readout module with a dual scale for depth and temperature, and a separate scale for conductivity; a 200 foot multi-conductor underwater cable; and a sensor unit

---

[1] Measurements of the physical parameters were also not taken during this period because the T.D.C. Monitory system did not operate below 0°C. Underwater temperature measurements were taken, however, during this period using a thermometer immediately following each photographic series.

consisting of a thermistor, a Bourdon tube potentiometric transducer, and a platinum-coated conductivity cell. The ranges of the T.D.C. system were 0^{o} to 40^{o}C, with an accuracy of $\pm$ 0.5^{o}C (temperature); 0 to 100 meters, with an accuracy of $\pm$ 1.5% (depth); and 10 to 80 millimhos/cm., with an accuracy of $\pm$ 2% (conductivity).

Procedure:

Before beginning the use of the T.D.C. monitoring system, the system was standardized against a 3% solution of NaCl, and an accurate thermometer, and all components were found to read to the desired accuracy.

Field Operation

The cable of the T.D.C. monitoring system was marked at intervals of 5 meters by use of plastic film tape. Prior to every use of the T.D.C. monitoring system in the field, the system was zeroed using calibration plugs of a specified resistance. For field operation, the sensors were placed within a protective sensor mounting tube and weighted with five pounds of lead. The sensors were lowered over the side of the boat[1] until they were just submerged. Readings were taken in this order: depth, temperature, conductivity. The values were recorded on sheets of Crona-flex film. The sensors were next lowered to the first marker (5 meters) where the measurement and recording precedure were repeated. Similarly, measurements were taken at 10 m., 15m., 20 m., 25 m., and 30 m. The maximum depth in the study area was 31 m. To sample these parameters, the line was permitted to

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[1] Refers to either the M.S.R.L.'s "TEAL", a rented trap skiff, or a dory.

become slack. The T.D.C. values were checked as the sensors were lifted and returned to the surface, stopping at each 5 meter interval. When a discrepancy between the 'descending' and 'ascending' values occurred, the whole procedure was repeated, beginning again at the surface.

B-III.1 (ii). Dissolved Oxygen Determination

Water samples were taken at 0, 5, 10, 20, 25, 30 and 31 meters, using a Van Dorn water sampler. Dissolved oxygen concentrations were determined using a modified Winkler procedure as outlined in Strickland and Parsons (1968) with the following modifications:

1. In place of 300 ml. B.O.D. bottles, 250 ml. reagent bottles which held a sample volume ranging from 280-295 ml. were used. Glass stoppers were modified (i.e. inserted end cut at angle) so that no air would be present in the water sample.

2. By use of 5 ml. automatic pipettes (P2023), 1.5 ml. quantities of manganous sulphate and alkaline potassium iodide were added immediately after filling the reagent bottles. Similarly, 1.5 ml. of sulphuric acid were added after the samples had been removed from darkness and been allowed to warm to room temperature.

3. A 100 ml. treated sample was transferred to a conical flask via a modified volumetric flask.

4. Fisher-certified concentrated solutions of sodium thiosulphate were used to make up 1 liter of stock solution of 0.1 N $Na_2S_2O_3$ rather than using dry thiosulphate crystals. Stock

solutions were diluted to 1 liter quantities of 0.0125 normality[1] which were used for titration.

5. Standardization of thiosulphate was performed every time a new solution was made up, using a 0.0125 N solution of potassium dichromate as described by Barnes (1959), to ensure that the concentration of $Na_2S_2O_3$ was exactly 0.0125 N. Each sample was titrated using a Metrohm Herisau Dosimat, an electrically operated 25 ml. burette. The digital scale of the Dosimat read out the number of mls. of titrant used to two decimal points.

---

[1] This concentration of sodium thiosulphate was calculated from an equation in Barnes (1959), in order that 1 ml. of titrant was equivalent to a concentration of 1 mg. of dissolved oxygen per liter of sample (or 1 part per million).

ie.

$$C = \frac{n \cdot F \cdot 1000}{2f}$$

where C is the oxygen content in mg-atoms O_2/liter
n is the volume of $Na_2S_2O_3$ in ml
F is the normality of thiosulphate
f is the volume of the sample

Let C_o = concentration of dissolved oxygen in the sample in mg./liter.

Since $\frac{C_o}{16} = C$, the equation becomes $\frac{C_o}{16} = \frac{n \cdot F \cdot 1000}{2f}$

Therefore, $C_o = \frac{16n \cdot F \cdot 1000}{2f} = \frac{8nF1000}{f}$

Since f = 100, therefore $C_o = 80\ n\ F$

Let $C_o = n$ (in order that the concentration of dissolved oxygen be equivalent to the number of mls. of thiosulphate).

Then $80\ F = 1$ and $F = \frac{1}{80} = 0.0125$

Therefore the normality of thiosulphate required was 0.0125 N.

B-III.1 (iii). Relative Irradiance (R.I.)

Measurements of R.I. were taken using a relative irradiance meter manufactured by Hydro Products (Model No. 420) which collected values of light intensity from two sources: an underwater photo-electric sensor (sea cell), and a gimballed surface photoelectric sensor (deck cell). Values which were read on the surface monitor were an expression of the sea cell sensor voltage as a percentage of the deck cell sensor voltage, thus giving relative irradiance. Calibration and operation of the system was carried out as outlined in the "Operation and Maintenance Manual" which accompanied the R.I. meter.

Field Operation

Prior to and after each use of the meter, its accuracy was checked using a number of calibrated screens which allowed light of a specific intensity to fall on the photoelectric sensor of the sea cell.

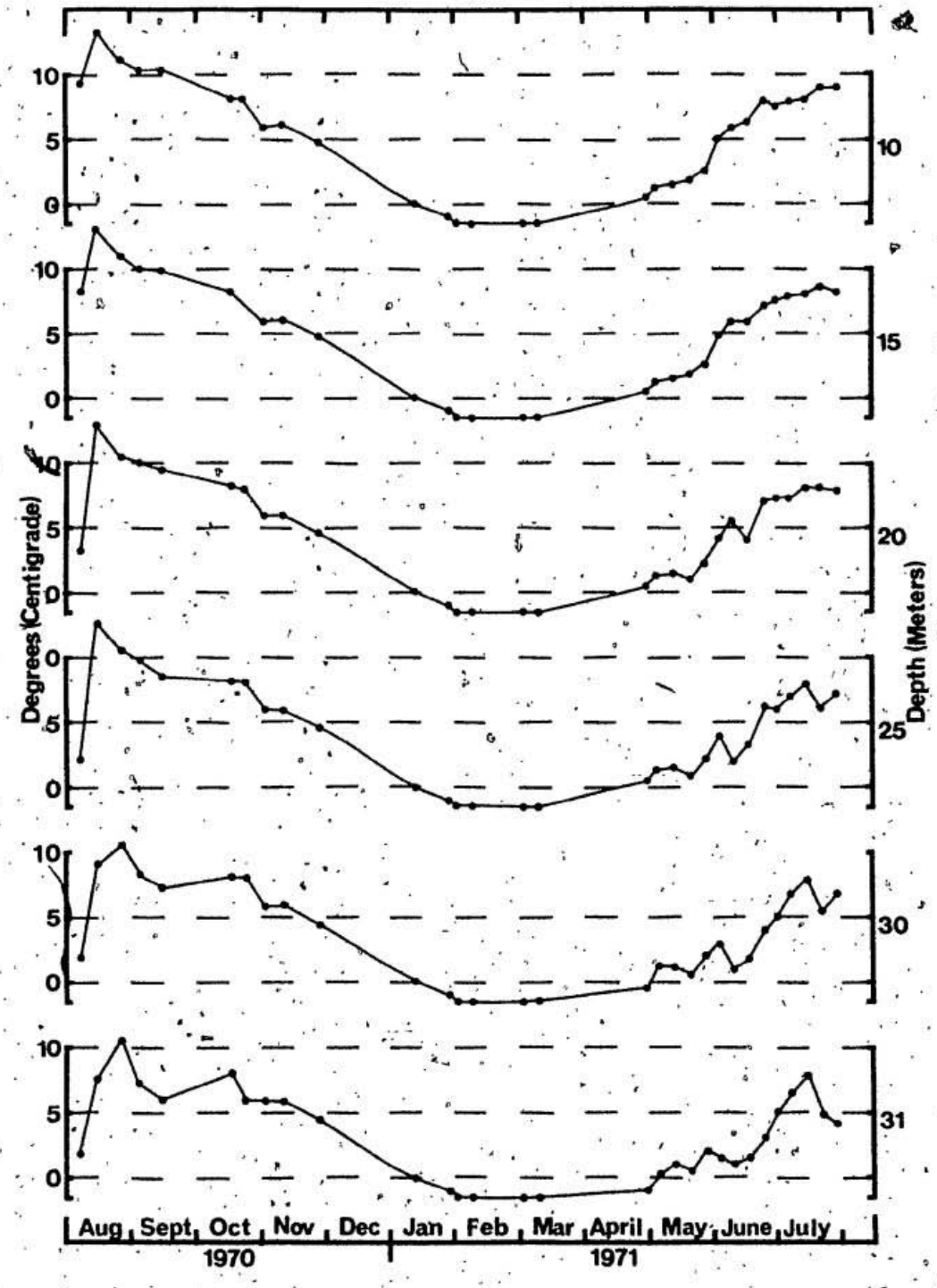
The cable, being marked as the T.D.C. cable, was lowered over the side of the dory, such that the position of the sea cell was horizontal and facing upward. Measurements were taken over the sand bottom area at depths of 5, 10, 15, 20, 25, 30 and 31 meters.

B-III.2. Results and Discussion

B-III.2 (i) Temperature

Fig. 12 summarizes the temperature regime of the study area, showing temporal changes in temperature as experienced at 10, 15, 20, 25, 30, and

Figure 12. Annual temperature regime of the study area at six depths. Data are presented in Appendix A.


Degrees (Centigrade)
Depth (Meters)
10
5
0
10
15
20
25
30
31
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
April
May
June
July
1970
1971

31 meters. Data, from which fig. 12 is drawn are presented in appendix A. The yearly temperature characteristics can be summarized as follows:

1. Pronounced cyclic changes in temperature ranged from a yearly summer maximum of 13.2°C to a winter minimum of -1.5°C.
2. A gradual cooling took place following the yearly maximum in August until a minimum of -1.5°C was established in January. Following the minimum which lasted throughout February and March, a gradual increase returned temperatures to near those of the previous year (1970).
3. Thermal stratification was poorly established for most of the year. From October 15 to May 26, the maximum vertical temperature range was 2°C.
4. For the period June - September, a variable degree of thermal stratification occurred ranging from an almost isothermal condition (July 14) to a pronounced thermocline August 6, showing a decrease in temperature of 5°C over a 5 meter depth interval.
5. Temperature fluctuations may be very sudden during the June - September period, establishing thermoclines in the study area for very short periods of time. Readings taken every minute for 16 mins. on August 14 with the probe resting on the bottom showed a range of 4.8° to 8.5° C.
6. In general, thermal stratification did occur to some extent during the temperature maximum period but the thermocline appeared to be deeper than the study area for the most part.

B-III.2 (ii) Salinity (Conductivity)

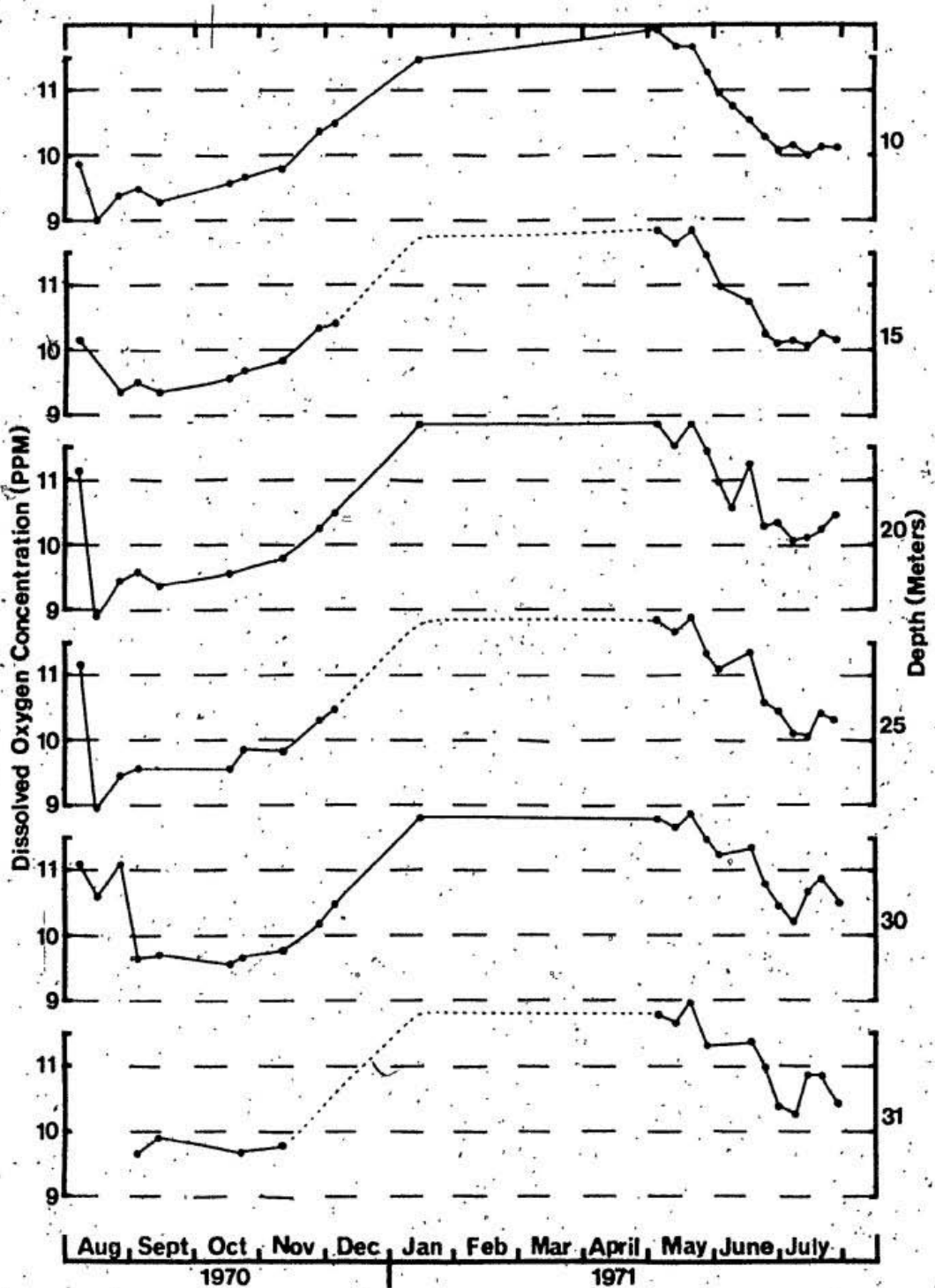
Conductivity readings are not presented because of a suspected breakdown in the probe. Although the probe was calibrated electronically before every operation, values, when plotted over the year period, showed a gradual decrease. When calibrated again against standard solutions at the end of the study, the probe was found to be reading approximately 5 millimhos/cm. too low. This decrease in efficiency appeared to take place over an extended period of time; hence the values could not be corrected. A study of the ranges exhibited by conductivity between 10 and 31 meters of each sampling date showed a similar annual variation as shown by temperature, i.e. a small range in October - May, and larger range from June - September.

B-III.2 (iii) Dissolved Oxygen Concentration

Fig. 13 outlines the dissolved oxygen-time relationship at depths 10, 15, 20, 25, 30 and 31 meters. Data from which fig. 13 was drawn, are presented in appendix C. The yearly dissolved oxygen regime can be summarized as follows:

1. Dissolved oxygen varied inversely with temperature; hence, the O_2-time curve is a mirror image of the temperature-temporal distribution.
2. Little vertical stratification was shown during the months October - May, whereas varying degrees of vertical stratification were shown during June - September.

Figure 13. Annual dissolved oxygen concentration regime of the study area at six depths. Data are presented in Appendix C.


Dissolved Oxygen Concentration (PPM)
Depth (Meters)
11
10
9
10
15
20
25
30
31
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
April
May
June
July
1970
1971

B-III.2 (iv). Relative Irradiance

Light could not be measured on a regular basis because of problems associated with a malfunctioning R.I. meter.Only one sampling series is shown in fig. 14 which was taken July 20, 1971. To determine the relationship between light and depth, the R.I. (y) and depth (x), data were fitted to the equation $y = ae^{bx}$ using the Wang Computer programme for least square fit. The derived equation was $y = 51.0e^{.1x}$ with a correlation coefficient of .993. Periodic changes in RI took place over the course of the study, but the importance of these changes cannot be assessed quantitatively. Factors such as angle of sun, cloud cover, and presence or absence of suspended material and algal blooms may alter this pattern. In summary, no assessment of periodic changes in relative irradiance could be monitored. Data for this series is presented in appendix D.

B-III.2 (v). Water Disturbance[1]

Introduction

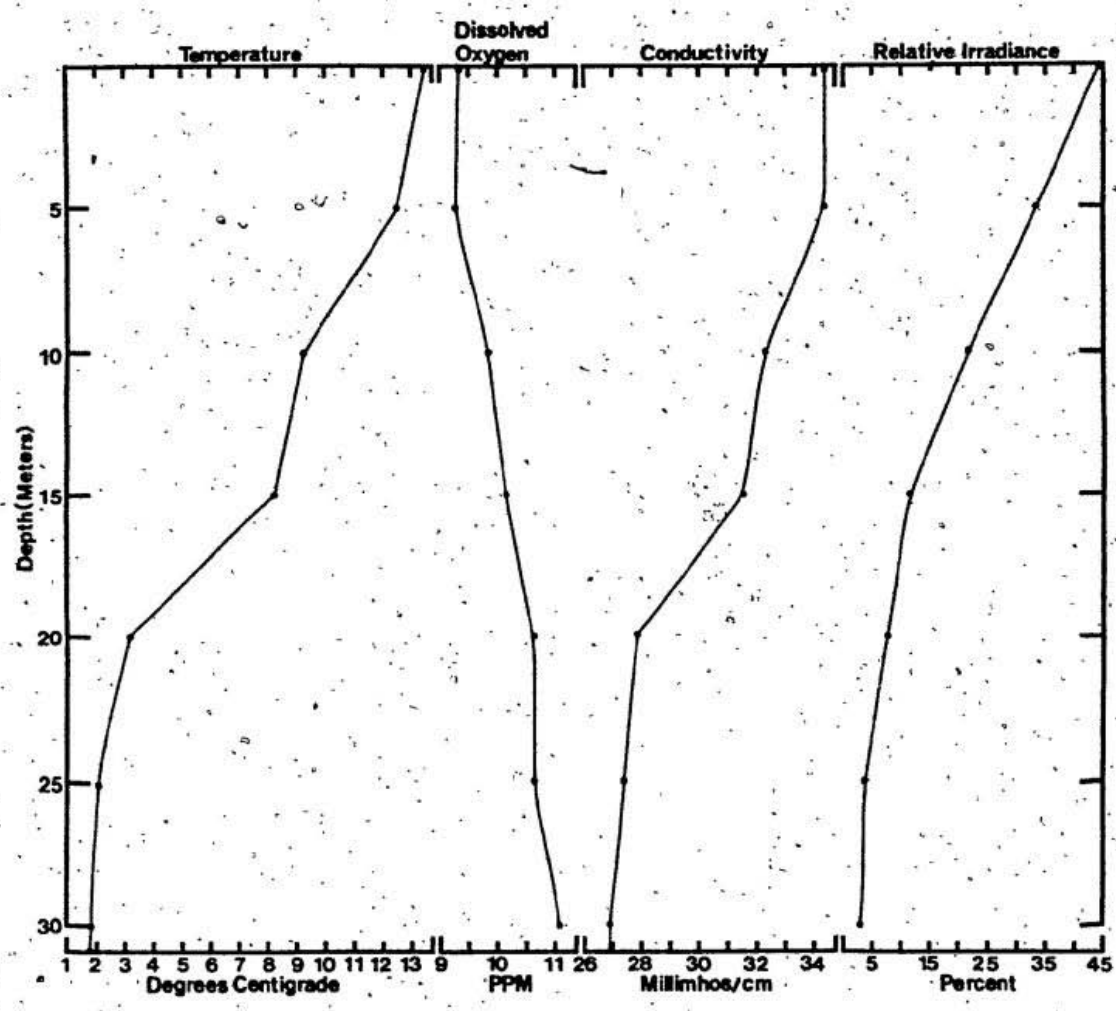
A variety of reasons[2] prevented a systematic study of this parameter during the study period. Hence an alternate strategy was employed of utilizing previously published data and applying the theoretical knowledge of waves to determine relative values of water

---

[1] The term "Water Disturbance" is used throughout this thesis as meaning any movement of water particles that would bring a force to bear on an asteroid.

[2] The major factor preventing such a study was the unavailability of equipment necessary to carry out a detailed sampling programme to determine the spatial and temporal changes in this parameter.

Figure 14. Graph depicting the maximum vertical stratification of temperature, relative irradiance, dissolved oxygen concentration, and conductivity in the study area. Data are presented in Appendices A, B, C, and D.


Temperature
Dissolved Oxygen
Conductivity
Relative Irradiance
Depth (Meters)
5
10
15
20
25
30
1 2 3 4 5 6 7 8 9 10 11 12 13
Degrees Centigrade
9 10 11
PPM
26 28 30 32 34
Millimhos/cm
5 15 25 35 45
Percent

disturbance in different locations in the study area for various times of the year. The following three relationships with respect to water disturbance were considered:

1. The effect of depth on degree of water disturbance.
2. The effect of topographic features of the bay (with particular attention to the study area) on the distribution of water disturbance within the study area.
3. Temporal changes in the amount of water disturbance present in the study area.

Since water disturbance, as defined (see footnote), would involve a wide range of causal factors including currents, tides, and wave dynamics, the difficulty in dealing with this factor would be enormous. Therefore, only the most influential factor, wave dynamics, is considered in this discussion.

1. The Effect of Depth on Water Disturbance.

The wave theory developed by Stokes (1847) and Lamb (1932) based on an ideal fluid, states that the free surface of the wave approximates the form of a trochoid.[1] Water particles in a wave, the form of a trochoid, according to Sverdrup (1942), describe circles which decrease in radius and velocity with increasing depth according to the following equations:

---

[1] "The curve which is formed by the motion of a point on a disc when this disc rolls along a level surface." (Sverdrup et al, 1942, pg. 526).

$$r = ae^{-2\pi \frac{z}{L}}$$

$$v = \frac{2}{T} ae^{-2\pi \frac{z}{L}}$$

r = radius of circle

a = amplitude of wave

L = wave length

T = period of wave

z = depth

v = velocity

From these equations it can be seen that not only does water movement decrease exponentially with depth, but also that water movement at a particular depth is dependent upon wave characteristics such as wave length, period, and amplitude. This latter relationship means that short period waves have a greater proportionate effect in shallow water than in deeper water than would long period waves. Since short period waves (ie. 4 sec. waves) are of more frequent occurrence than long period waves (8 sec. or greater), the effects of depth on water distubrance is again magnified when considering the accumulative effects of water disturbance over a year period.

2. The Effect of Topographic Features of the Bay on Distribution of Water Disturbance.

In the last section, the depth-water disturbance relationship was considered without any consideration of the effect of the bottom on wave characteristics. This section deals primarily with the relationship between slope and water disturbance.

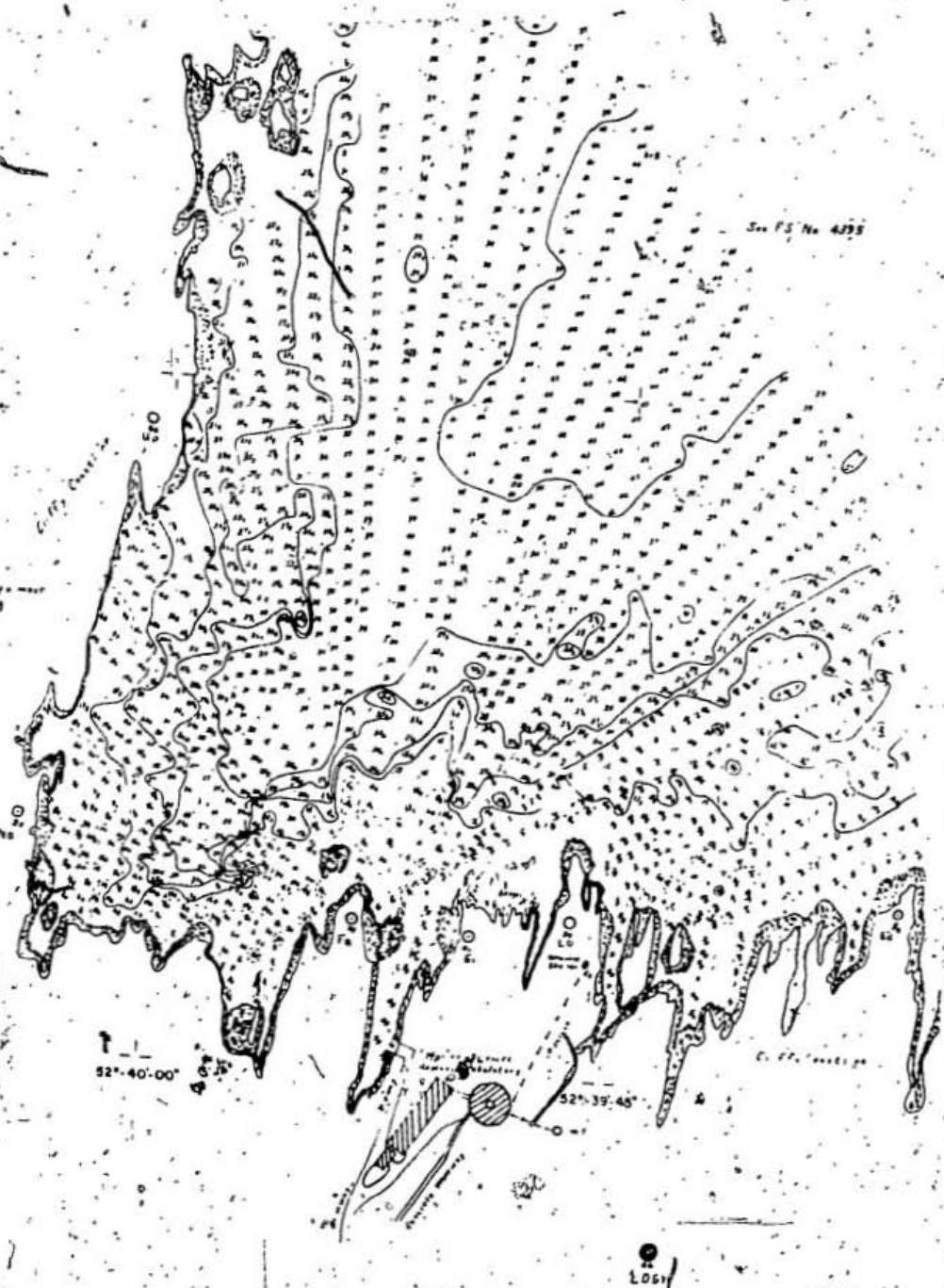
Since the coastline of Logy Bay (fig. 15) extends in a northerly direction on one side (Red Cliff) and in an easterly direction on the other, the effects of waves from the northeast were considered to be the most important. Waves from the northeast direction having periods of seven seconds and nine seconds impinging on the study area were considered in terms of both the reflective and refractive characteristics of the cliff. By means of a series of calculations, it was determined that the cliff had relatively no reflective effect on an incoming wave. As the wave passes in over the cliff, however, the wave would tend to be refracted inwards towards the cliff onto the plateau.

Waves from the north and east would also contribute wave components that move across the plateau. Many of these components would break in the area of Mad Rock. Runback resulting from the transportation of the water mass onto the plateau would tend to run off the plateau, down the cliff, into the trench at the base of the cliff, and continue in a northeasterly direction out of the bay. This pattern would tend to explain the sand build-up at the base of the cliff. As water moves down the slope it would tend to be turned outwards at the steep slope changes, and the outflow at the trench bottom. Hence areas of steep slope (area C and E) would tend to have less water disturbance per se than areas of lesser slope due to runback down the cliff.

3. Temporal Changes in Water Disturbance.

Calculations of the amount of wave energy entering Logy Bay from the east, northeast, and north directions were made with a

Figure 15. Map of Logy Bay showing depth contours (in meters).
(Refer to Figure 8 for position of the study area.)


See FS No. 4393
52°-40'-00"
52°-39'-45"

planimeter from Wave Spectrum Charts, published by the Bedford Institute based on 1970 data (Table 2).

These relative values show that the major period of high wave energy occurred during the August to April period. During the period from May to August no energy was contributed to the study area from this source. Peak water disturbance occurred during October and again in March and April. March and April may have been affected by ice conditions to reduce this effect within the bay.

Summary and Empirical Diving Evidence

Based on theoretical computations, the amount of water disturbance within the study area would demonstrate a large degree of variation according to depth-water disturbance, slope-water disturbance, and time-water disturbance relationships.

Diving observations indicated the validity of each relationship. During periods of high water disturbance, the decrease in the amount of water disturbance with depth was most evident. Many studies in the MAL zone and Area B on the cliff were prevented because of high water disturbance, but studies in areas C, D, and E would be carried out very easily. The practice of 'diving under' depths of high water disturbance was often followed.

Decreased water disturbance in areas of steep slope was supported by the amount of debris in each area. Most evident in this relationship was the high number of Mytilus edulis shells found on ledges in areas C and E (steep areas) as opposed to the low number of shells observed

Table 2. Wave spectrum energy entering Logy Bay for each month of the year (1970).

Since the values of Wave Spectrum Energy are calculated by means of a planimeter from Wave Spectrum Charts, no specific units can be given to these values. Values indicate relative amounts of energy entering the bay for each month.

Month	N	NE	E	Total
January	0.00	0.01	0.01	0.02
February	0.00	0.00	0.00	0.00
March	0.03	0.02	0.02	0.07
April	0.05	0.01	0.02	0.08
May	0.00	0.00	0.00	0.00
June	0.00	0.00	0.00	0.00
July	0.00	0.00	0.00	0.00
August	0.00	0.00	0.00	0.00
September	0.02	0.01	0.01	0.04
October	0.07	0.02	0.01	0.10
November	0.02	0.02	0.00	0.04
December	0.01	0.00	0.00	0.01

in areas B and D. The complete lack of debris on the sand bottom indicated the existence of an outward flowing current over the sand bottom.

B-IV. Biota

B-IV.1. Methods for Determination of Biota

B-IV.1 (i) General Observations of Flora and Fauna

For both the MAL zone and the cliff area, general observations were made of the species components, habitats, and general distribution and abundances of the flora and fauna. These observations were made at various times throughout the study.

B-IV.1 (ii) Photographic Analysis

The distribution of only a few selected organisms inhabiting the cliff area were quantitatively determined by means of analysis of a film taken on October 20, 1970 for the determination of sea star distribution. The materials and methods for producing this film are discussed later in section C.II.1 (i). Numbers of Strongylocentrotus droebachiensis (O.F. Muller) and Gersemia sp. were counted per photograph, and the area occupied by Didemnum albidum (Verrill) was calculated by counting squares of known area covered by D.albidum in each photograph. Relative abundances of two algal species dominant to the cliff area were approximated.

B-IV.1 (iii). Hand Sampling Technique

During the months of September, October and November, 1971, a series of nine dives were completed to sample the major benthic invertebrates of the transect area using a 0.25 meter quadrat square. The quadrat

square was constructed of dexion, and had the dimensions 0.25 m X 0.25 m (±0.002m).

To take the samples, diver B[1] held the quadrat square in position on the bottom so that the TL was flush with and parallel to the right side of the square and the top right corner was in line with the numbered marker on the TL.

Diver A then removed and counted specimens, one species at a time, making recordings on Crona-flex sheets. A stainless steel spatula was employed by diver A to remove organisms from crevices. Any organism which could not be identified was placed in a small finely meshed sample bag and brought back to the M.S.R.L. for identification. Colonial organisms were recorded with a + or - indicating their presence or absence, the numbers of solitary individuals being counted and recorded.

B.IV.2. Results & Discussion

B-IV.2 (i) MAL Zone

A high abundance of biota is supported in the MAL zone of which the major algal components are Alaria esculenta and Laminaria digitata, with Mytilus edulis being the major faunal component. Alaria esculenta was dominant in the more exposed shallower areas such as around the base of Mad Rock. Moving away from this centre, its numbers decreased and was displaced by L.digitata which extended to the fringes of the plateau.

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[1] Diver A refers to the author and Diver B refers to the diving partner.

Random clumps of M.edulis covered approximately 50% of the bottom of the plateau. Clumps ranged in size from 50-100 individuals covering an area of diameter less than half a meter, to many thousand individuals covering areas of 5-10 meters in diameter. In all clumps, individuals were extremely closely packed representing a narrow range of sizes from recently settled individuals to a maximum length of 40 mm. Examination of data collected by Mr. R. Scaplen during a survey of M.edulis populations in protected areas around the coast of Nfld., showed this size range to be extremely small.

Encrusting biota covered the remainder of the substrate. The chief components of the encrusting forms were corralline algae mainly Phymatolithon laevigatum (Foslie) and Clathromorphum circumscriptum (Stomf). Some areas of the bottom were also covered with the yellow sulphur sponge, Halichondria panicea (Pallas).

In general, molluscs were very abundant in the MAL zone. Large numbers of Lacuna vincta (Montagu) and Margaretes helicinis (Phipps) were found on L.digitata and A.esculenta. Three other gastropod species were represented, but to a lesser degree. Of these species, Buccinum undatum L., the common northern whelk, and Thais lapillus (L.), the dog whelk, were found often in areas of shelter such as crevices and dips in the substrate, whereas the northern limpet, Acmaea testudinalis (Muller) was randomly distributed in low abundance over the entire plateau. Chitons, chiefly Tonicella marmorea (Fabricius) were observed both on the encrusting corallines and on shells of M.edulis.

Seasonally, nudibranchs, principally Doto coronata (Gmelin), Coryphella rufibranchialis (Johnston), Aeolidea papillosa (L.), Dendronotus

albus (Asconius) and D.frondosus (Asconius). Onchidoris fusca (Muller) O.aspersa (Alder and Hancock) and Tergipes tergipes (Johnston) are very abundant in this area and are found on a variety of substrates, eg. hydroids, Metridium senile.(L.), coralline algae, and mussel shells.

Many organisms take advantage of the microhabitat provided by the settlement of silt between mussels and at the bases of the large kelps. The major components are the arctic saxicave, Hiatella arctica (L.), the daisy-brittle star, Ophiopholis aculeata (L.) and polychaetes such as Nereis pelagica L. and the scaleworm, Lepidonotus squamata (L.).

The last two major components of the MAL zone are the common sea anemone Metridium senile, and the green sea urchin Strongylocentrotus droebachiensis. Both species reached high abundance in certain areas of the zone, M. senile being very common in the mussel beds and sea urchins abundant in crevices.

B-IV.2 (ii). Biota of the Cliff Area

B-IV.2 (iia) General Considerations

Since the biota of the cliff area demonstrated a high degree of variation with depth and slope, the floral and faunal components of differing areas of the cliff are presented to show these relationships. Data are presented in three ways:

1. General and qualitative description of the flora and fauna as derived from photographic analysis are presented as abundance per TLQ.

2. Results of 0.25 X 0.25 m hand sampling technique are presented as abundance per TLQ.
3. General observations of abundances, distributions and habitats of the fauna as determined from photographic analysis, hand sampling techniques, and periodic observations made over the course of the study are summarized.

Results

B-IV.2 (iib) Photographic Analysis

Since organisms of small size, drab colouration, and/or low abundance could not be considered for photographic analysis, only the distributions of Strongylocentrotus droebachiensis, Didemnum albidum, and Gersemia sp., and two algal species, Agarum cribosum (Mert) and Ptilota serrata (Kutz) are presented (Table 3). General description of these results are combined with general observations of these species in section B-IV.2 (ii,d).

B-IV.2 (ii,c) Hand Sample Technique

The hand sample technique only proved useful in determining the relative abundance-distribution patterns of the more abundant species. Since a small sample size was employed in this study, samples cannot be considered entirely representative of the depth or slope of the area in which they were taken. Both of these difficiencies, ie. the inability to deal with low abundance, and the non-representative nature of the samples, are considered in the next section. Table 4 summarizes only the ten most abundant species as determined by this method. Other fauna observed and recorded during this study are also presented in the next section.

Table 3. Abundances per TLQ of selected organisms found in the Cliff Area as determined by photographic analysis.

---

[1] Number of individuals per 1.0 X 1.5 meters.

[2] Area of bottom covered in $cm.^2$

[3] Relative abundance: + low, ++ medium, +++ high.

TLQ No.	Strongylocentrotus droebachiensis[1]	Gersemia sp.[1]	Didemnum albidum[2]	Agarum cribosum[3]	Ptilota serrata[3]
1	79	-	-	++	+
2	54	-	-	+++	+
3	125	-	-	+	-
4	217	-	-	-	-
5	99	-	-	+	+
6	35	-	-	++	+
7	56	-	-	+	+
8	131	-	-	-	-
9	82	-	-	-	+++
10	53	-	-	-	+++
11	110	-	-	-	++
12	111	-	-	-	+
13	91	11	-	-	+
14	108	7	-	-	+
15	95	5	13.85	-	++
16	70	-	-	-	+++
17	87	1	-	-	++
18	59	-	-	-	+++
19	12	-	72.70	-	+++
20	12	-	60.15	-	+++
21	34	-	34.95	-	+
22	71	-	110.15	-	+
23	139	-	17.70	-	+
24	145	-	18.35	-	-

Table 4. Numbers of individuals of the ten most abundant fauna (excluding asteroids) per 0.0625 square meter, as collected by the hand sampling technique.

TLQ No.	Metridium senile	Tonicella marmorea	Other anemone species	Hyas araneus (L.)	Ophiopholis aculeata	Margaretes costalis (Gould)	Pagurus sp.	Acmaea testudinalis	Hiatella arctica	Mytilus edulis
1	18	-	2	-	1	-	-	1	-	4
2	36	4	-	-	-	-	-	2	-	5
3	23	-	-	-	-	-	-	5	-	-
4	32	5	-	-	4	-	-	-	6	-
5	64	-	-	1	-	-	1	-	-	-
6	82	-	-	2	1	-	-	-	1	-
7	134	-	-	2	3	-	-	-	1	-
8	108	-	1	3	-	-	-	-	1	-
9	75	1	1	-	1	-	-	-	-	-
10	44	6	-	1	-	-	1	-	-	-
11	50	-	1	4	-	-	1	-	-	-
12	20	3	-	1	-	-	-	2	-	-
13	7	4	-	-	-	1	1	-	-	-
14	8	4	3	1	-	-	3	-	-	-
15	14	2	1	2	-	1	-	-	-	-
16	7	-	3	2	-	1	-	-	-	-
17	22	2	2	1	-	1	2	-	-	-
18	2	9	2	-	-	1	2	-	-	-
19	17	-	4	-	-	1	-	-	-	-
20	12	-	-	-	1	1	-	-	-	-
21	8	1	-	-	1	2	-	-	-	-
22	7	2	-	-	-	1	-	-	-	-
23	20	5	3	1	-	1	-	-	-	-
24	3	-	4	-	-	-	-	-	-	-
	813	48	27	21	12	11	11	10	9	9

B²IV.2 (ii,d) General Observations and Summary of Fauna

Cnidaria

Representatives of this phylum were very abundant over the entire cliff area. Metridium senile, the common sea anemone was clearly the most abundant macro-benthic organism. In certain areas such as TLQ's 7 and 8, M.senile formed almost solid mats of individuals. Comparison of data obtained during the hand sampling technique showed that it was more than six times more abundant than the second-most abundant species (Strongylocentrotus droebachiensis, not shown in Table 3[1] had a total count of 128 as compared to 813 for M.senile). Its distribution pattern was skewed towards shallow water with major aggregations on the steep slope of area C.

Other species of anemones were observed frequently in the cliff area; however, identification of these species was not made. It appeared that the larger species of anemones were found in the deeper water area of the cliff area (area E).

Hydroids were very abundant over the entire cliff area. Most obvious of these species was Obelia geniculata (L) which had such a high abundance on Agarum cribosum as to make the surface appear fuzzy. Hydroids attached to the substrate were most obvious in area E.

The soft coral (alcyonarian) Gersemia sp. as evident from the photographic data was most abundant in area D, an area of lesser slope.

---

[1] Numbers of S.droebachiensis are not listed for this survey because it was felt that they were more accurately estimated by photographic analysis.

Echinodermata

Over the entire cliff area, the green sea urchin, S.droebachiensis was a very common representative of the benthic fauna. In numbers it ranked second to M.senile of the macro-benthic animals, but probably represented the highest single species contribution to the biomass. Data presented from the photographic analysis showed a general decrease in abundance with depth, with large concentrations of individuals at the rock-sand interface. This distribution pattern appeared valid for the entire cliff area.

Ophiopholis aculeata was generally very poorly represented in the cliff area; however, large aggregations of individuals were observed wherever sufficient protection from predators was to be found. Such areas were crevices, closed spaces between animals (such as Volsella modiolis (L)), under rocks and debris, and between the thalli of Lithothamnion glaciale (Kjellm). Aggregations could be found at any depth in the cliff area; however, the largest aggregations were observed in area B, an area of high concentration of L.glaciale.

Sea cucumbers were very poorly represented in the cliff area. Of the holothurians, Cucumaria frondosa (Gunnerus) was most abundant, but its abundance was less than one per 10 square meters of bottom. Only two Psolus fabricii (Duben & Koren) were observed in the entire cliff area, and both of these were being fed upon by sea stars (Crossaster papposus). Borrowing apodous sea cucumbers, Chirodota leavis (O.Fabricius) were observed occasionally in silt that formed under rocks found along the sand-rock interface.

Annelida

Polychaetes were of low abundance in this area. Nereis pelagica and Lepidonotus squamata were observed in the shallower water areas, chiefly area B in similar locations as those described for Ophiopholis aculeata.

The leathery tubes of Fabricia sabella (Ehrenberg), a sabellid worm, were often observed attached to the substrate, predominantly in areas D and E.

Arthropoda

Crustaceans were very abundant in the cliff area. Pagurus sp. the hermit crab, utilizing empty shells of Margaretes costalis (Gould), was most abundant in area D, an area of gentle slope. Individuals were generally of small size and were restricted to horizontal or gently sloping surfaces.

Throughout the entire cliff area, Hyas araneus (L.) was very abundant and was observed mostly in cracks or crevices of the substrate.

Ectoprocta

Bryozoans as a group demonstrated a high degree of species diversity and were generally distributed in relatively high abundance throughout the cliff area. Forms varied from the flat encrusting type which covered shells, algae, and substrate, to the arborescent type such as Flustra foliacea (L.), which attached to practically any available substrate. Both forms could be observed in all areas of the cliff area, but as a general rule, encrusting forms were observed most often in shallow water, and the arborescent types on the more steeply sloping areas (C and E).

Urochordata

As was observed for ectoprocts, the species diversity of the phylum Urochordata was very high. Tunicates were found in all areas of the cliff area but reached their highest abundance and diversity in area E. The most numerous tunicate was Didemnum albidum which formed large white encrusting flat colonies and was very frequent in occurrence in area E.

Mollusca

Owing to the importance of this group as asteroid prey, a great degree of attention in this study was centred on the distribution, abundance, and habitat of the members of this phylum. Table 5 summarizes these aspects of their distribution.

Table 5. Distributions, relative abundances, and habitats of the molluscs observed in the Cliff Area.

L - low M- medium

[1] Depth ranges listed are the total depth ranges observed for these species in the study area. Note that area B, as defined earlier, begins at a depth of 8.7 meters.

Molluscs	Depth Range (meters)[1]	Area of Maximum Abundance in Cliff Area	Relative Abundance in Cliff Area	Microhabitat
Amphineura				
Tonicella marmorea	0-31	no specific area	M	substrate, shell surfaces, etc.
Gastropoda				
Acmaea testudinalis	0-10	B	L	substrate
Thais lapillus	0-10	B	L	substrate
Buccinum undatum	0-15	B	L	substrate
Margaretes heliclinus	0-15	B	M	algae, substrate
Lacuna vincta	0-15	B	M	algae, substrate
Margaretes costalis	20-31	D & E	M	substrate
Bivalvia				
Mytilus edulis	0-10	B	L	substrate, *M. edulis* shells
Volsella modiolis	5-10	B	L	substrate, *M. edulis* shells, cracks
Chlamys islandica (O.F. Muller)	25-31	E	L	substrate (motile)
Hiatella arctica	0-31	A & B	M	cracks, burrowed in any soft substrate
Anomia aculeata O.F. Muller	0-31	no specific area	M	substrate, shells
Musculus discors (L.)	25-31	E	L	cracks

C. Asteroid Distribution

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C. Distribution and Abundance of Asteroids in the Study Area

C-I. Introduction

Asteroid abundance-distribution patterns were determined independently for the cliff area and for the MAL zone. In the cliff area, sea star abundance-distribution patterns were determined by means of a quantitative analysis of a series of photographs taken weekly (when possible) along the transect line. In the following sections (C-II.1 (ii)), the apparatus, diving procedure, and techniques of film analysis used to determine the spatial and temporal distributions of the sea stars found in the cliff area, are outlined. Materials and methods for the determination of the asteroid distribution and abundance in the MAL zone are presented in section C-III.2. Cliff Area

C-II.1. Materials and Methods for Determining Asteroid Distribution in Cliff Area

C-II.1(i) Introduction

Sloped rocky bottoms, such as the cliff area, pose serious problems for the field biologist with respect to quantitative sampling techniques. Traditional methods, such as sampling from surface vessels, simply cannot be employed because: (a) a cliff presents a small horizontal surface making it difficult for accurate location of samples, and (b) even specially designed mops and dredges run into serious problems on rock surfaces. Since the study area was relatively small, it was preferable that specimens not be removed so that estimates of changes in temporal distribution could be accurately monitored.

To overcome these difficulties, an intensive diving survey was undertaken using photography as the tool so that no removal or disturbance of animals was necessary. Other potential advantages in adopting

photographic techniques were:

1. A permanent record of abundance and distribution of sea stars can be obtained.
2. Observations of other aspects of sea star biology in their natural environment can be noted.
3. The area sampled can be easily calculated.
4. The location of the photograph can be accurately determined.
5. Sizes of organisms can be measured.
6. Spatial relationships between sea stars and between other organisms can be examined.

C-II.1 (ii) Apparatus, Diving Procedures, and Film Analysis

Since an exact picture size is required for quantitative analysis, photographs must be taken at a constant distance from the substrate. In order to achieve this requirement, the camera, a Nikon F with a 35 mm F/2.8 lens and fitted with a Hugy-Fot underwater housing, was mounted at the apex of a specially constructed photographic tower (figs. 16 & 17). The tower, 2.2 meters in height, was constructed of aluminum dexion, and at the base, an aluminum frame, 1.5 X 1.0 (± 0.005) meters, was mounted. A scale consisting of alternate strips of red and white tape (each 5 cms. in width) was attached to the upper surface of this frame for the purpose of determining the size of the photographed organisms. Therefore, through the viewing lens, it was possible to see a clearly delineated area of 1.5 X 1.0 meters[1] with a size reference afforded in each viewing field by the scale.

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[1] Calculation of the distance between the camera and the frame, required to include the entire area bounded by the frame, was made underwater because water has a higher index of refraction than air.

Figure 16. Underwater photograph of the photographic tower and divers taken during a photographic series.

(photographed by Dr. J.R. Strickler)

Figure 17. Underwater photograph of the photographic tower showing the positions of camera and housing.
(photograph taken by Dr. J.R. Strickler)

Since all pictures required artificial light, a Braun F 280 electronic flash in a Hugy-Fot housing (fig. 18) was used, attached to the photographic tower approximately 1.2 meters above the measured frame. The film used was Kodak Daylight High Speed (ASA 160) Ektachrome. Buoyancy floats (fig. 18) were attached to neutralize the weight of the frame underwater.

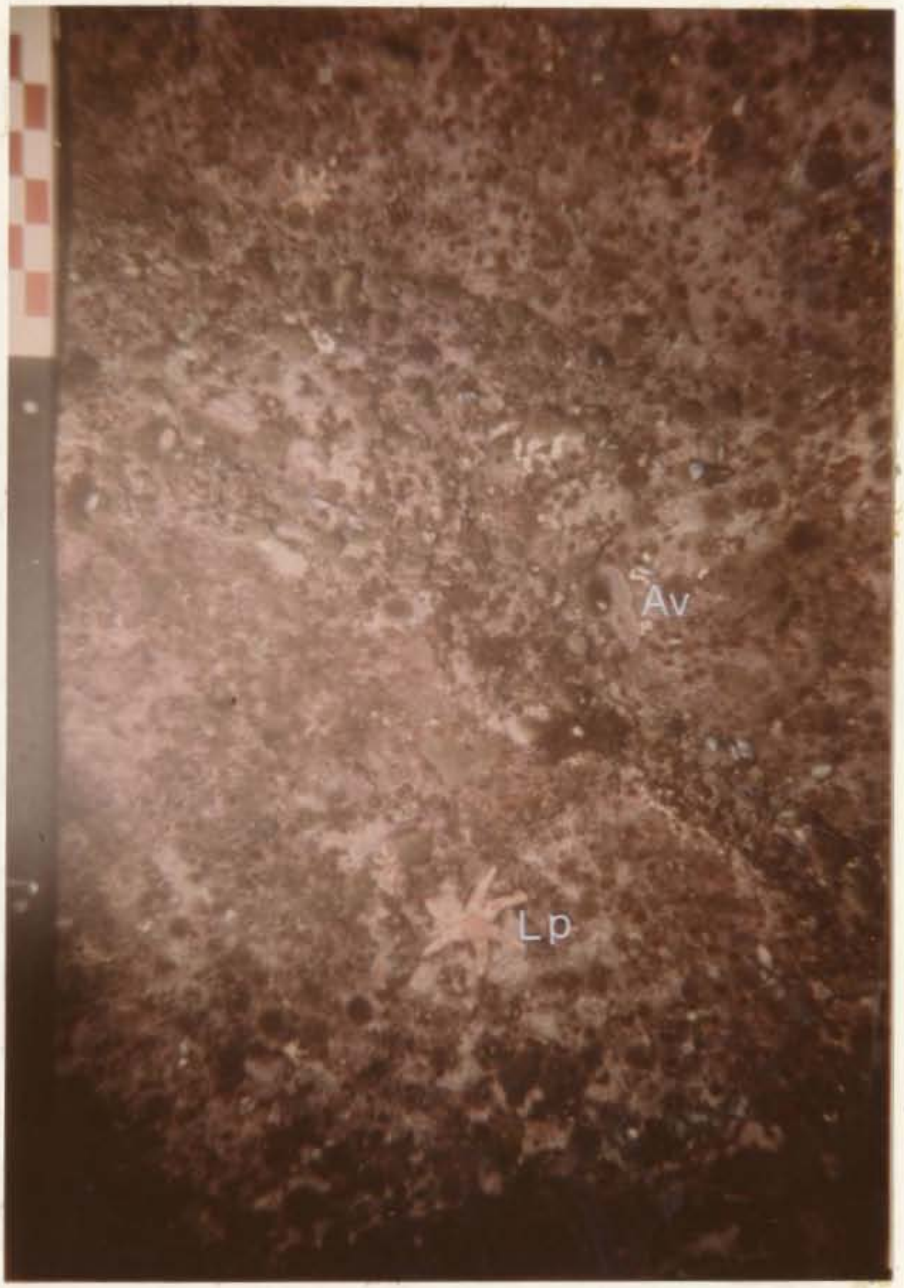
In order that an exact location of each picture was known, pictures were taken along the TL. Each picture was taken such that the 1.5 meter side of the measured frame was parallel to and flush with the TL (fig. 19), with its upper right and lower right corners placed exactly over the poxy putty markers at each numbered tag. The numbered tag was inserted between two slotted pieces of plywood attached to the frame to indicate the position of each picture on the TL. Pictures were taken in sequence beginning at TLQ 1 and continuing to TLQ 24.

During the diving procedure, diver A (the author) was positioned at the apex of the frame to trigger and rewind the camera, and diver B (diving partner) was located at the base to help with positioning of the frame (fig. 16). Care was taken by both divers throughout this procedure to avoid disturbing sea stars (either by the movement of the divers' fins or by the tower itself). The tower was returned to the surface by filling a second buoyancy float from the regulator of diver A.

A complete photographic series, ie. TLQ's 1-24, was taken once a week when possible between July 30, 1970, and July 28, 1971. During this sampling period a total of 35 series was obtained. Reasons for missed series were several and varied, including rough seas making

Figure 18. Underwater photograph of photographic tower showing the flash housing and flotation bags.
(photographed by Dr. J.R. Strickler)

Figure 19. Representative photograph of a typical TLQ taken at TLQ 8 during a photographic series, Oct. 5, 1970. Note the red and white scale (5 cm intervals) at the upper left, and several individuals of Leptasterias polaris (Lp) and Asterias vulgaris (Av).


Av
Lp

diving impossible, and phytoplankton blooms reducing the water clarity so as to make photography impossible.

Films were developed and analysed in the uncut film strip form. Each film strip, then, represented the one meter wide, 36 meter long, strip of bottom which extended along the left side of the TL. Film strips were analysed by projection by means of a Bell and Howell film strip projector onto a sheet of bristol board. Measurements of all sea stars were taken using calipers and compared with a predetermined scale to ascertain the actual size of each starfish. Recordings were made on printed data sheets of the species and size of every specimen found in each TLQ. Any sea star with its entire central disc inside the measured frame was considered in the sample. If the measured frame allowed only part of an individual to be visible, it was recorded as being in the sample if it was observed along the left and top margins of the frame and not recorded if it was observed along the right and bottom margins. Species identification was based on colour, shape, number of arms, and size, in addition to other recognized taxonomic features. Sea stars which could not be identified were measured and denoted 'unknown'.

The size (R) of an individual starfish was determined by measuring the distance from the centre of the central disc to the tip of the longest straight arm. No measurements of size were taken when either of these points was not clearly visible. One procedure was followed which was an exception to this. Sea stars which did not have any straight arm visible were measured by taking the sum of a number of straight line segments around the curvature of the arm.

C-II.1 (iii). Efficiency of the Photographic Sampling Method

Since the resolution of pictures obtained from the photographic series was found to vary between 0.2 and 0.4 cm., no estimate of sea stars measuring less than 0.5 cm. could be made. A small random error may also have existed in numbers of observations in that sea stars greater than 0.5 cm. may have positioned themselves in such a manner that they were not visible to the camera. Since the substrate was relatively free of particulate matter and other hiding places, most of this error was removed by subtracting areas obscured by algae, shadows, air bubbles, etc, such that the abundance of sea stars was expressed as the number of individuals per area of unobscured bottom. Subtraction of obscured areas generally did not bias the sample because the actual obscured area in each TLQ was not constant over time. For example, areas obscured by algae may be unobscured in the next photographic series because an alga fixed at one point is continually in motion because of water disturbance. Similarly, shadows rarely were observed in the same location.

A large error factor, however, was introduced in species identification. Of all asteroids observed, 20.5% could not be identified. Individuals of small size provided the greatest difficulty for identification. Only 2.1% of the unidentified sea stars were greater than or equal to 1.5 cm. In order to exclude this identification error due to size for A.vulgaris and L.polaris, only specimens greater than or equal to 1.5 cm. were included in the sample. Since all C.papposus, S.endeca, and Henricia sp. individuals identified were greater than 1.5 cm., their abundance estimates were not affected. Exclusion of individuals

belonging to the species H.eschrichti smaller than 1.5 cm., however, was not performed because most of its population was smaller than this size. Identification of this species for individuals of small size was easier than for A.vulgaris and L.polaris because of its bright colouration. Hence, only a small error factor was felt to be associated with this size discrimination with respect to the spatial and temporal abundance estimates of H.eschrichti.

In order to calculate the relative abundances of the asteroid species, A.vulgaris, L.polaris, and H.eschrichti, the assumption was made that the proportions of each species population not sampled because of these size discriminations were approximately equal.[1]

Errors in size measurements as a result of the uneveness of the surface of the substrate, prevented accurate assessment of the size of the sea stars from the photographic analysis. Measurements of 25 equally sized (10 cm.) metal rods photographed on a representative irregular bottom had a coefficient of variation of 7.5 and a maximum error of 14.3%. Hence, size measurements were not utilized to assess growth or size frequency distributions.

---

[1] The proportions of size of each species sampled, ie. $\frac{\text{minimum size sampled}}{\text{maximum size sampled}}$ were $0.182\left(\frac{0.5\text{ cm.}}{2.15\text{ cm.}}\right)$ $0.182\left(\frac{1.5\text{ cm.}}{8.25\text{ cm.}}\right)$ and $0.130\left(\frac{1.5\text{ cm.}}{11.5\text{ cm.}}\right)$ for H.eschrichti, A.vulgaris, and L.polaris, respectively, thus indirectly justifying the validity of this assumption.

C-II.1 (iv) Representativeness of the Photographic Sampling Method

As defined in section B, the study area was an area of bottom which represented a high degree of horizontal uniformity in terms of substrate, slope, and faunal constituents. An assumption was made that the transect line area was representative of the sea star distribution of the entire cliff. To test this assumption, the distribution of sea stars on the left and right sides of the transect area were compared.

For four sampling dates (July 30, August 6, August 13, and August 24, 1970), duplicate photographic series were made of the left and right sides of the TL. So that corresponding pairs could be directly compared, left and right sides of the same areas of the TL were photographed during the same dives. Each photograph was analyzed as outlined in section C-II. 1(ii), and abundances were converted to number of individuals per square meter of unobscured bottom. A paired t-test (Wang programme) was applied to the abundance of L.polaris for the four sample series at all TLQ's.

The t-values obtained for the overall analysis for 95 degrees of freedom was 1.218 and had a probability of 0.774 (Wang t-distribution) on the t-distribution. Hence, the null hypothesis that no significant difference existed between the sample means was accepted.

The proximity of the two samples and comparison of only one species are definite limitations to the validity of the conclusion that the sampled area was representative of the cliff area. However, comparison with other areas of the cliff area was not possible

because of the permanent nature of the TL. L.polaris was considered to be representative of the sea stars of the cliff area because it had the highest abundance and would demonstrate the highest degree of variability of its distribution had it proved to be non-uniform.

C-II.2. Spatial Distribution (Cliff Area)

C-II.2 (i) General Considerations

Since sample size per sampling date was small (ie. a low number of individuals per species per TLQ), spatial distribution for each sampling date could not be considered. In order to achieve a clear pattern of abundance-distributions, a full year time period was considered so that any seasonal variation between species could be examined. Since each TLQ represented a unique set of physical, chemical, and biological properties, distributions were examined with respect to these divisions. Although values are expressed in absolute terms (ie. number of individuals per square meter of unobscured bottom), only the relative abundances of each species with respect to TLQ's are considered significant. Since temporal variations in abundance existed (resulting possibly from migration, natality, and mortality), absolute values determined from the year mean cannot be considered representative of any one time period within the year.

C-II.2 (ii) Asteroid Relative Abundance with Respect to TLQ's

Relative abundance (R.A.) values were calculated from the yearly mean data (ie. no. of individuals per sq. meter of unobscured bottom), expressing the abundance of each species as a percentage of the total asteroid abundance (the total number of identified asteroids). For example,

Relative Abundance of L.polaris for TLQ 1 =

$$\frac{\text{mean no. of ind. per sq. m. unobscured bottom TLQ 1) (Append. E) X 100}}{\text{total abundance of all identified sea stars}}$$

Although these values were calculated for all species, only the four most abundant species, L.polaris, H.eschrichti, A.vulgaris, and C.papposus, are shown in fig. 20.

An examination of fig. 20 shows four distinct patterns:

I. TLQ's 1-5. Area of extreme L.polaris dominance.

II. TLQ's 6-18. Area of reduced L.polaris dominance.

III. TLQ's 19-23. Area of H.eschrichti dominance.

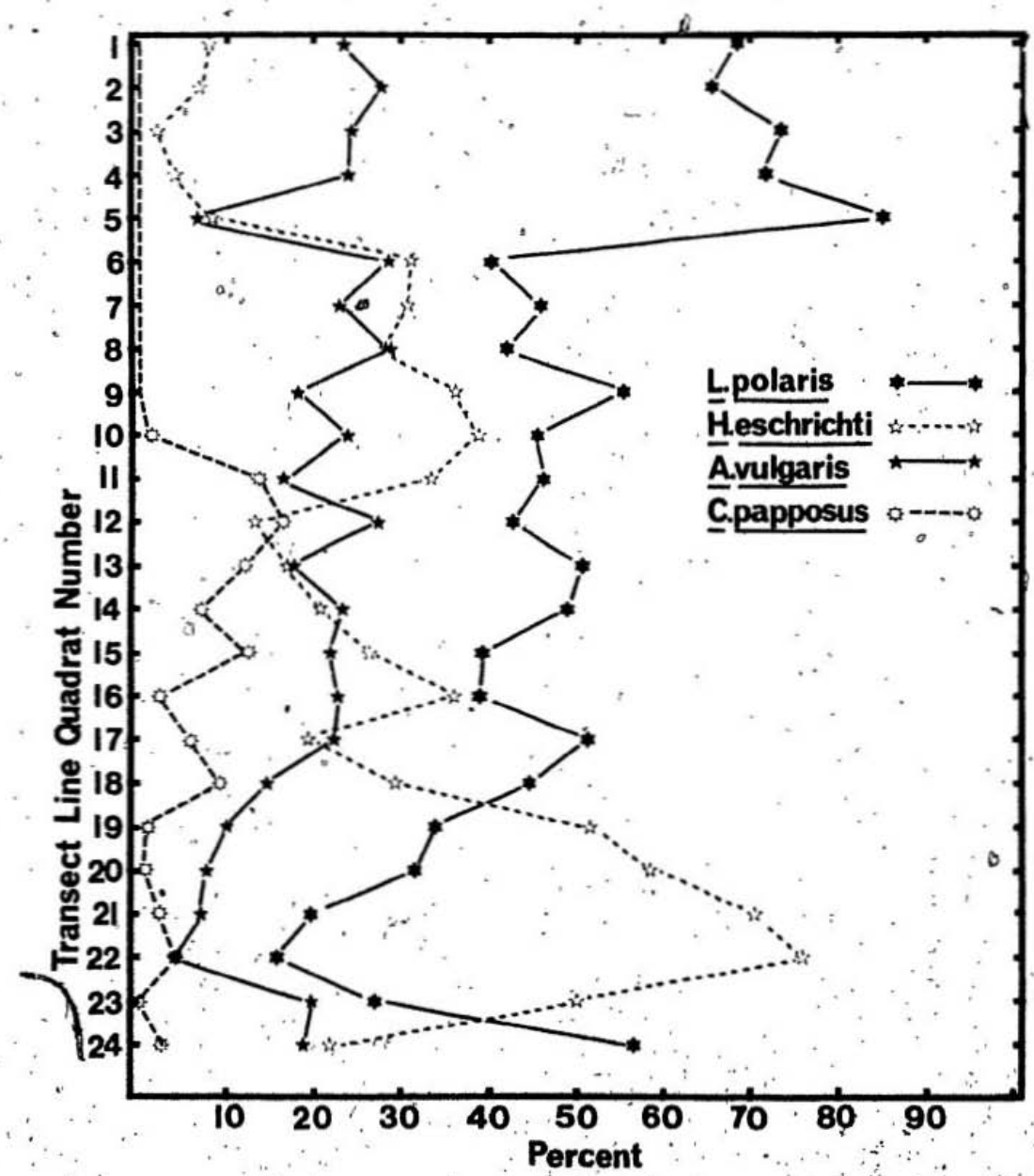
IV. TLQ 24. Area of reversed dominance.

I. Area of Extreme L.polaris dominance (TLQ's 1-5). L.polaris represented in this area, a high proportion of the asteroid population, ranging from a 'low' at TLQ 2 of 67.4% to a peak at TLQ 5 of 87.3%. Except for a significant drop to 4.2% at TLQ 5, A.vulgaris was the second most abundant species displaying relatively constant RA values of 21.8 - 25.3% from TLQ's 1-4. H.eschrichti displayed a low RA value in this area, never exceeding 8.4% of the total asteroid count. Only at TLQ 5, did it exceed that of A.vulgaris.

II. Area of Reduced L.polaris Dominance (TLQ's 6-18).

Although L.polaris was consistently the most abundant species in this area, it represented less than 50% of the total asteroid count in all TLQ's except TLQ 9. Relatively constant values of RA, ranging from 39.1 - 54.6% existed for L.polaris throughout this area. Similarly, A.vulgaris demonstrated a roughly constant RA with values ranging from 14.0 - 28.0%. H.eschrichti, however, had variable RA

Figure 20. Graph of the relative abundance (based on yearly mean abundances) of Leptasterias polaris, Asterias vulgaris, Henricia eschrichti, and Crossaster papposus, for each TLQ.


Transect Line Quadrat Number
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
10
20
30
40
50
60
70
80
90
Percent
L.polaris
H.eschrichti
A.vulgaris
C.papposus

values peaking at TLQ's 10 and 16, and was slightly more populous than A.vulgaris, being more abundant in 8 of the 13 TLQ's.

Even though C.papposus achieved its greatest abundance in this area (TLQ's 11-18), it ranked fourth in RA.

III. Area of Henricia eschrichti Dominance (TLQ's 19-23).

RA values of H.eschrichti began to rise at TLQ 17, but did not reach dominance until TLQ 19. Its abundance increased through to TLQ 22 where it peaked and then dropped off significantly again at TLQ 23. Throughout this range it accounted for over 50% of the total asteroid count,and scored a maximum RA of 77.0% at TLQ 22. Conversely, the RA values of A.vulgaris and L.polaris began to decline around TLQ 17, and reached 'lows' at TLQ 22. A slight upswing was measured for TLQ 23. Other species showed parallel RA's with L.polaris being approximately 25% higher than A.vulgaris. C.papposus demonstrated a lower RA in this area than it did in the previous one.

IV. Area of Reversed Dominance (TLQ 24)

L.polaris was again established as the dominant species with a high RA of 56.2%. H.eschrichti dropped off as the dominant species (RA 21.8%), and A.vulgaris had a similar RA of 18.8%. The RA of C.papposus increased slightly over the previous TLQ.

C-II.2 (iii) Absolute abundance (yearly means) with respect to TLQ's

In order to compare the distribution of each species with the unique set of physical, chemical, and biological factors associated with each TLQ, the absolute abundance (calculated on yearly means)

of each species was plotted against TLQ number. A consideration of the non-variable parameters of each TLQ (depth, slope, and distance from MAL zone) with respect to abundance is now presented.

Leptasterias polaris

In fig. 21, a plot of abundance of L.polaris (y) against TLQ (x), an overall decrease in abundance with increasing TLQ was evident. The plotted regression line has an equation of $y = 1.73 - 0.067x$ with a correlation coefficient of -0.834. A comparison with fig. 11 reveals that this relatioship can be related to either depth or distance from the MAL zone. Since each TLQ has a length of 1.5 meters, the TLQ-abundance graph in actuality is the same as an abundance-(distance from MAL zone) graph. The regression line plotted of abundance-depth, shown in fig. 22 has the equation $y = 2.27 - 0.07x$ with a correlation coefficient of -0.834. The equality in correlation coefficients of these two regression lines makes it impossible to determine with which factor abundance is best correlated, ie. depth or distance from the MAL zone (TLQ). Both factors show significant correlation to the 0.01 critical level (ie. critical level for n = 24 at P = 0.01 is 0.515)[1] and cannot be separated on the basis of this analysis.

Most of the variation, ie. as shown in the correlation coefficient, can be attributed to five anomolous TLQ abundances which have a large displacement from the regression lines. Greater than expected values of abundance occurred at TLQ's 1, 8 and 20, whereas,

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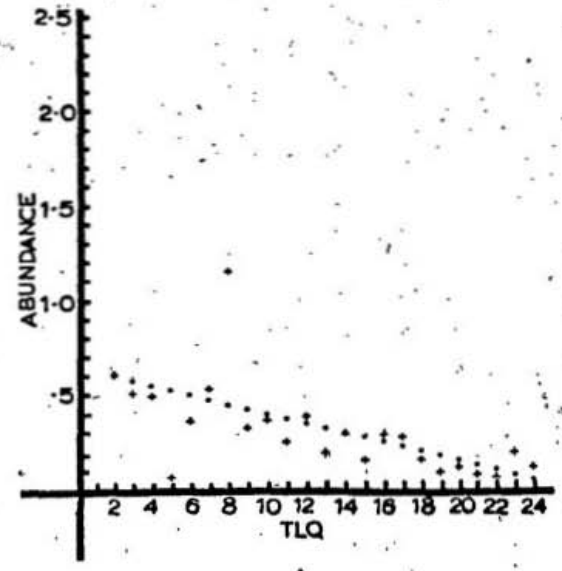
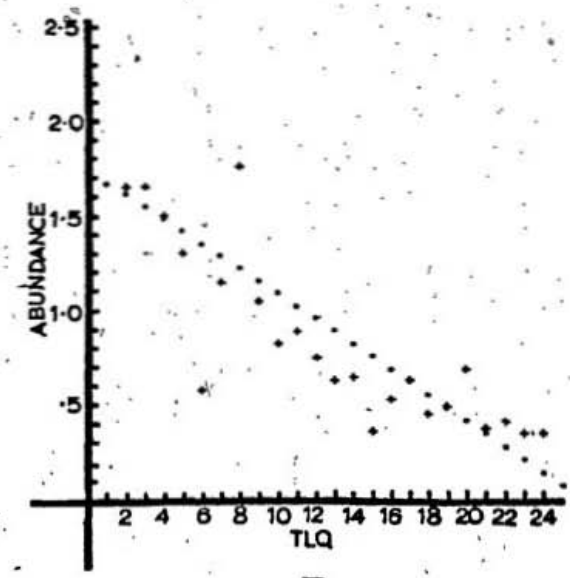
[1] Values from Statistical Tables, Sokal and Rohlf (1969).

Figure 21. Graph of absolute abundances (yearly mean) of Asterias vulgaris (A), Leptasterias polaris (B), Henricia eschrichti (C), and Crossaster papposus (D), with respect to TLQ's.

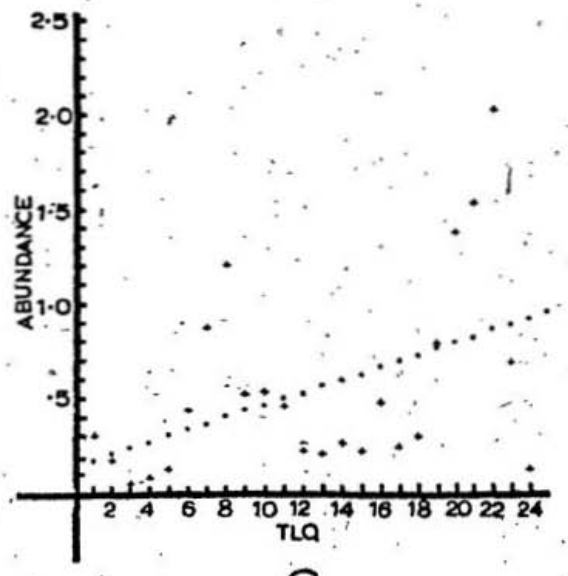
Abundances (indicated by +) are calculated as the number of individuals per square meter of unobscured bottom. Dotted lines in A, B, and C are the plotted regression lines. Refer to the text for equations.


ABUNDANCE
2·5
2·0
1·5
1·0
·5
2 4 6 8 10 12 14 16 18 20 22 24
TLQ

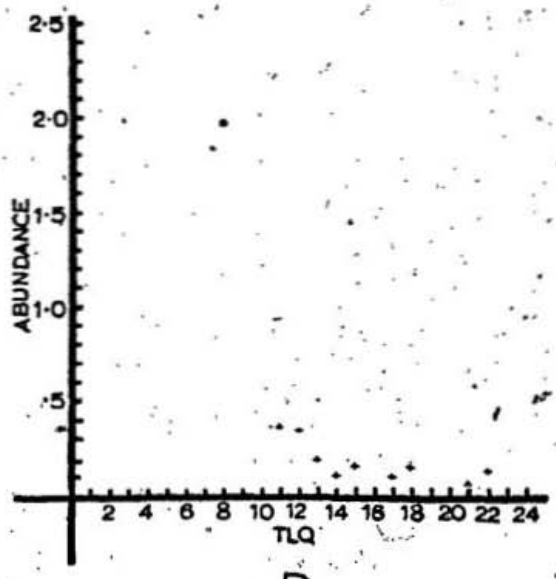
A


ABUNDANCE
2·5
2·0
1·5
1·0
·5
2 4 6 8 10 12 14 16 18 20 22 24
TLQ

B


ABUNDANCE
2·5
2·0
1·5
1·0
·5
2 4 6 8 10 12 14 16 18 20 22 24
TLQ

C

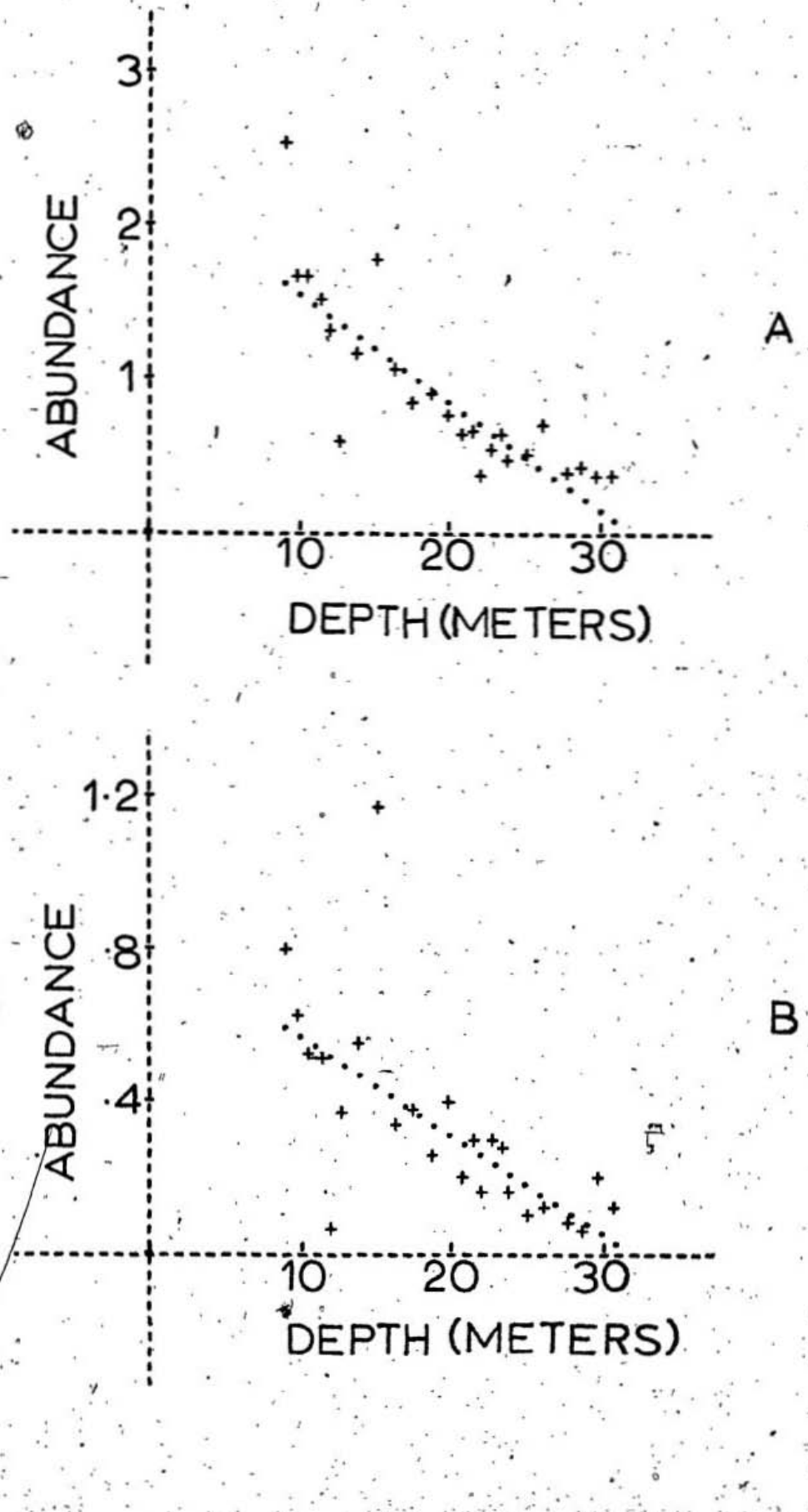

ABUNDANCE
2·5
2·0
1·5
1·0
·5
2 4 6 8 10 12 14 16 18 20 22 24
TLQ

D

Figure 22 A. Graph of the abundance (yearly mean) of Leptasterias polaris with respect to depth.

Figure 22 B. Graph of the abundance (yearly mean) of Asterias vulgaris with respect to depth.

Abundances (indicated by +) are calculated as the number of individuals per square meter of unobscured bottom. Dotted lines are the plotted regression lines (refer to the text for equations).


3
2
1
ABUNDANCE
10
20
30
DEPTH (METERS)
A
1·2
·8
·4
ABUNDANCE
10
20
30
DEPTH (METERS)
B

less than expected values occurred at TLQ's 6 and 15. Similarities in the position of TLQ's 8 and 20, and conversely the similarities in the position of TLQ's 6 and 15, suggest a relationship of abundance to certain topographic features. Fig. 11 showing the location of TLQ's, places TLQ's 8 and 20 on a steep downslope a short distance (1-2 meters) below a positive (increase) change in slope, whereas TLQ's 6 and 15 are located on more gently sloping areas below a negative (decrease) change in slope. An examination of the significance of these locations with respect to topography and water disturbance was presented in section B-III.2(v).

Asterias vulgaris

The general distribution pattern of A.vulgaris is similar to that of L.polaris indicating a decrease in abundance with increasing depth or TLQ number. The regression lines of abundance plotted against TLQ and depth are $y = 0.639 - 0.025x$ and $y = 0.837 - 0.026x$, respectively. As was the case for L.polaris, correlation coefficients of these regression lines were very similar -0.663 (TLQ) and -0.667 (depth) and were both within the 0.01 critical level of significance. Two anomolous abundances are shown by A.vulgaris at TLQ's 5 and 8 suggesting a similar relationship of abundance to specific topographic locations as shown by L.polaris.

Henricia eschrichti

An examination of fig. 21C reveals two possible relationships: an increase in abundance with depth (or increasing TLQ), and high abundances associated with steeply sloped areas, i.e. area C (TLQ's 7-12) and area D(TLQ's 19-24). The calculated linear regression lines for depth-abundance and TLQ=abundance ($y = -0.108 + 0.034x$, and

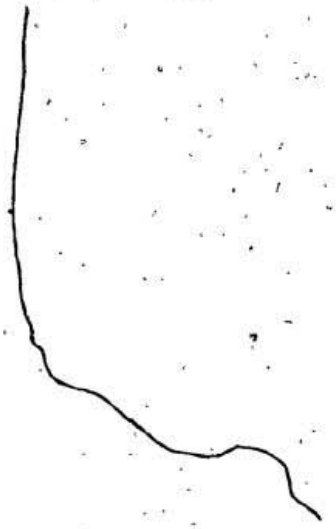
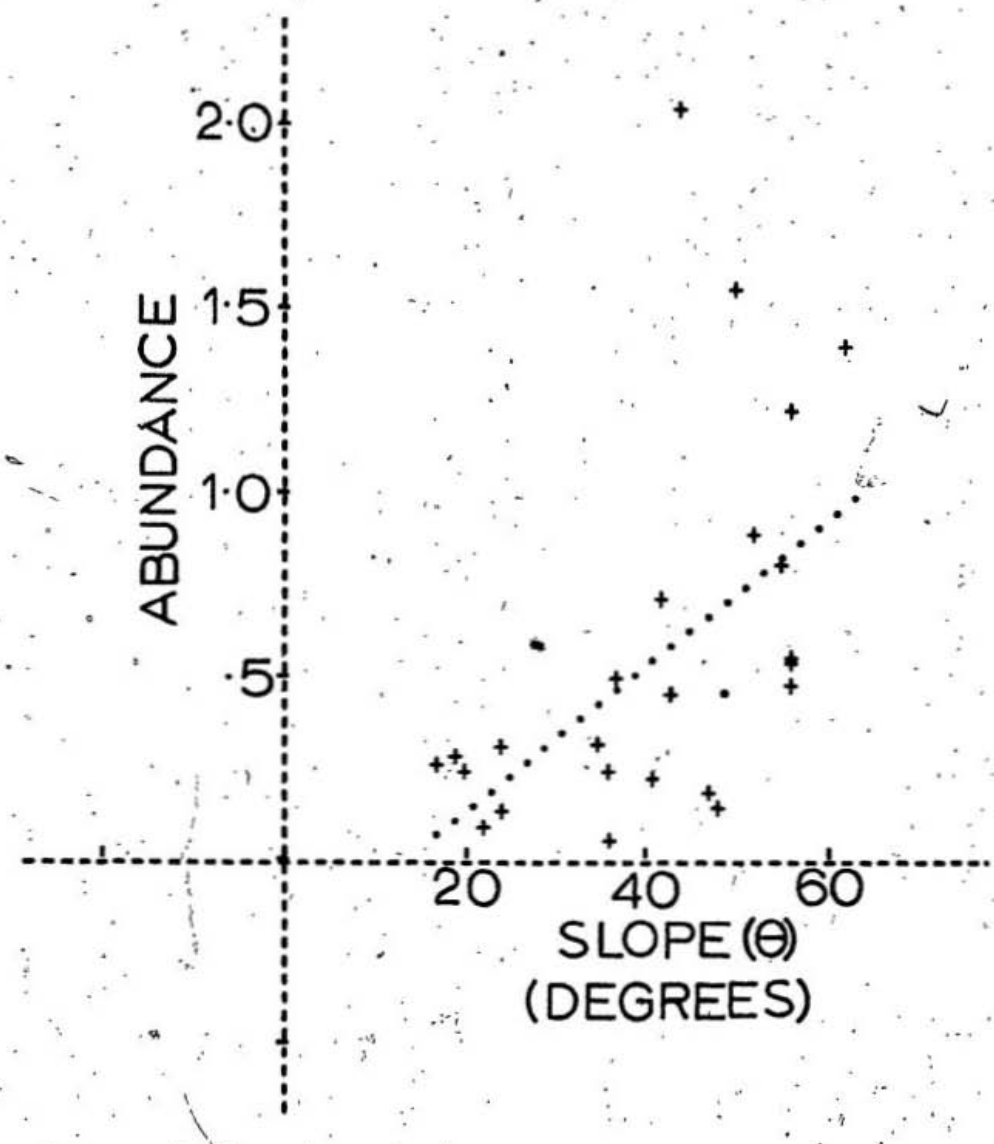


Figure 22 C. Graph of the abundance (yearly mean) of Henricia eschrichti with respect to angle of inclination, i.e. slope (θ).

Abundances (indicated by +) are calculated as the number of individuals per square meter of unobscured bottom. Dotted line is the plotted regression line (refer to the text for equation).


2·0
1·5
1·0
·5
ABUNDANCE
20
40
60
SLOPE (θ)
(DEGREES)

$y = 0.146 + 0.033\ x$) have low and similar correlation coefficients (0.443 and 0.455, respectively), from which it is impossible to determine with which parameter abundance is best correlated. As evident from fig. 21C, a high degree of displacement from the regression line exists and both regression lines are significant only to the 0.05 significance level ($P\ 0.05, n = 24 = 0.404$)[1].

Although much of this displacement can be related to increased abundance on steeply sloped areas, a low correlation (0.534) exists when a regression line is calculated for slope (mean angle of inclination for each TLQ) versus abundance. Fig. 22C, a graph of this relationship, shows that abundance does not correlate well with an absolute value of angle of inclination[2]. It appears, rather, that high abundances of H.eschrichti are associated with the more steeply sloped areas such that abundances peak near the midpoint of these steeply sloped areas decreasing moving away in either direction. On gently sloping areas, abundances are lower with area B having a minimum at the midpoint and area D remaining roughly constant. These tendencies appear to indicate that the distribution of H.eschrichti is more strongly related to the topographic features of the cliff area as defined by depth and slope, rather than absolute values of angle of inclination and depth.

Crossaster-papposus

In the study area, C.papposus was completely restricted to depths greater than 18 meters (TLQ 11) and demonstrated an oscillating pattern

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[1] Sokal and Rohlf, (1969) "Statistical Tables."

[2] This correlation is significant to the 0.05 level; however, this correlation appears to result from the tendency of H.eschrichti to concentrate on steeply sloped areas rather than a tendency to select to select a specific angle of inclination.

of distribution with maxima at TLQ's 11, 18, and 22, and minima TLQ's at 16, 19, 20 and 23.

Solaster endeca and Henricia sp.

The frequency of observation of these two species was so low that clear definition of their spatial (and temporal) distribution was not possible. Both species are listed in Appendix. A more comprehensive examination of the distribution of S.endeca is given in section D-II, a study of its movements.

Values, obtained from the photographic analysis, the migration and movement, and feeding studies, indicate that S.endeca is a deeper water species, never found above a minimum depth of 18 meters (TLQ 11).

The range of Henricia sp. (TLQ's 13-19) as determined from the photographic analysis is a poor indicator of its distribution. General observations of this species indicated that it could be found at any depth or position within the cliff area. No determination of the range of maximum abundance could be made on the basis of these observations.

Conclusions

As we have seen in this section the spatial distribution patterns of asteroids found in the cliff area showed significant differences between species, both in the relative abundances of each species with respect to TLQ's and in the absolute abundance with respect to TLQ values recorded for each species. Also evident was that the distribution patterns of each species could be described

in terms of location with respect to depth and slope or distance from the MAL zone. Although some variation in spatial distribution was apparent with time, each species is compared for equal time periods. Hence, comparisons of the spatial distribution patterns to determine species differences are valid.

C-II.3. Temporal Distribution (Cliff Area).

C-II.3(i) General Considerations

In order to establish whether any temporal variation existed in sea star distribution patterns for separate periods of the year, the TLQ's were divided into four sections so that sufficiently large numbers of each sea star species could be examined for each sample date. Equal sized areas of six TLQ blocks were chosen coinciding with the major areas differentiated on the basis of slope (ie. areas B, C, D, E, fig. 11). Abundances were calculated as the number of individuals of L.polaris, A.vulgaris and H.eschrichti per square meter of unobscured bottom and were plotted against time.

Each of the four TLQ blocks was tested for 34 sample dates using a two-way analysis of variance[1]. In blocks where any part of the bottom was obscured (blocks 1-6 and 7-12), the number of individuals

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[1] Although a one-way analysis of variance was sufficient to determine changes in abundance with time, the two-way analysis of variance (Wang Programme) was used because of its easier mode of 'keying in' data. Since vertical (depth, TLQ) variation was considered in section C-II.2 (iii), these data are not presented here.

per square meter of unobscured bottom was used as the variable, whereas, in blocks 13-18 and 19-24, where no part of the bottom was obscured, the number of individuals per TLQ (1.5 sq. m) was used.

C-II.3 (ii) Results and Discussion

Areas which demonstrated significant temporal variation, i.e. TLQ blocks 1-6 and 7-12 for L.polaris, block 7-12 for A.vulgaris, and blocks 7-12 and 19-24 for H.eschrichti (Table 6), were those areas in which the yearly mean abundance of these species was highest (data are presented in the appendices E, F, G).

TLQ blocks showing a significant temporal variation (figs. 23, 24, and 29), can be interpreted as representing a series of periodic oscillations[1] varying in maximal and minimal abundance and time period. The following interpretations of oscillation patterns for these TLQ blocks were utilized to assess temporal changes in abundances of each species:

1. The amplitude of each oscillation indicates the degree of change in abundance.

2. The period of each oscillation indicates the time period over which the change in abundance occurred.

3. By examining maxima and minima of abundance in all oscillations over the sampling time period, a determination of net changes in the population dynamics of a species can be made.

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[1] An oscillation was considered to be any change in abundance considered significant which began at a low abundance (minimum), rose to a peak (maximum), and returned to a low abundance. An oscillation, then must extend over at least three sampling dates.

Table 6. Analyses of variance of the yearly distributions of Leptasterias polaris, Asterias vulgaris, and Henricia eschrichti for TLQ blocks 1-6, 7-12, 13-18, and 19-24.

N.S. - not significant

*** - significant to the 0.001 level

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1 TLQ 6 was mostly obscured by algae; hence, only a very small area of the bottom was visible. When the number of individuals observed for this TLQ was divided by the area of unobscured bottom to obtain the number of individuals per square meter of unobscured bottom, invalid estimates of the abundances of H. eschrichti were obtained. So that the analysis of variance was not biased, these sampling dates were excluded.

Species	TLQ Block	F-value	Degrees of freedom	Probability	Significance
Leptasterias polaris	1-6	10.985	5, 165	0.999	***
	7-12	5.615	5, 165	0.999	***
	13-18	1.291	5, 165	0.730	N.S.
	19-24	1.679	5, 165	0.836	N.S.
Asterias vulgaris	1-6	1.892	5, 165	0.902	N.S.
	7-12	9.240	5, 165	0.999	***
	13-18	0.786	5, 165	0.439	N.S.
	19-24	1.133	5, 165	0.655	N.S.
Henricia eschrichti	1-6	1.778	5, 145	0.879	N.S.
	7-12	9.596	5, 165	0.999	***
	13-18	1.536	5, 165	0.819	N.S.
	19-24	18.408	5, 165	1.000	***

Figure 23. Graph of temporal abundance of Leptasterias polaris in four TLQ blocks.

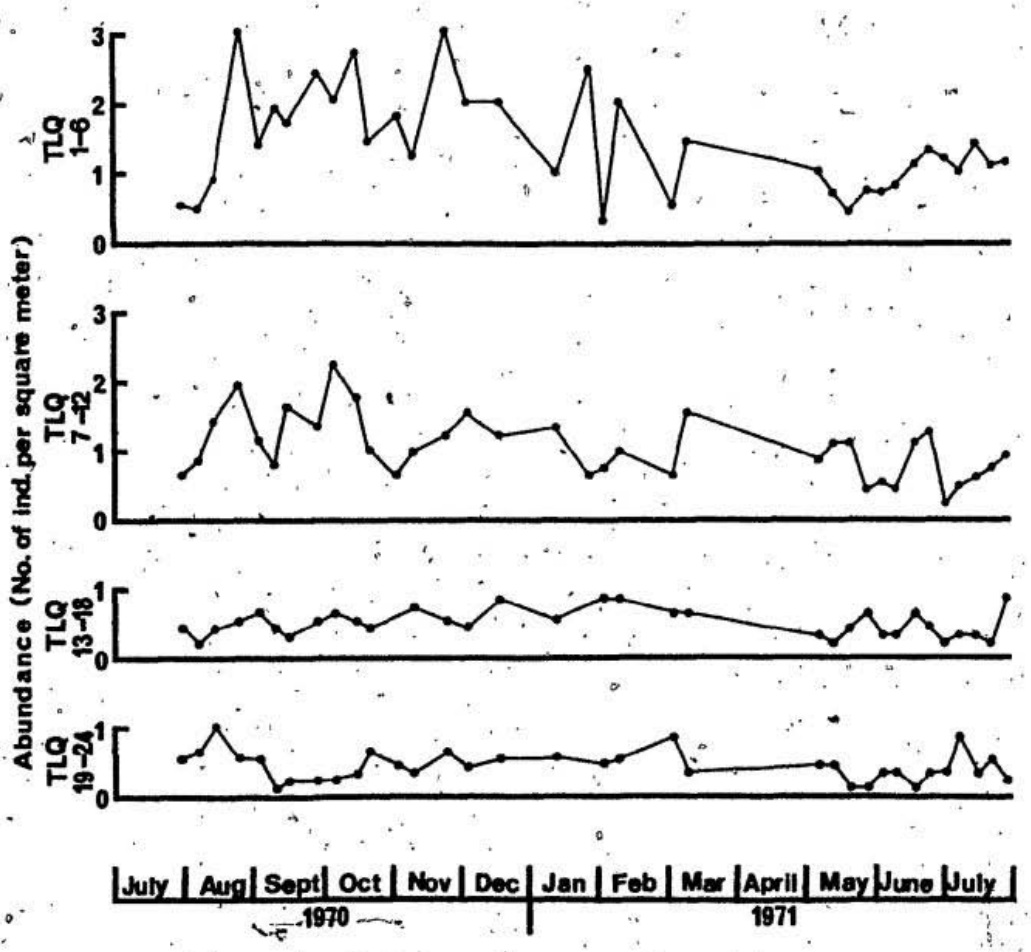

Abundance (No. of ind. per square meter)
TLQ 1-6
TLQ 7-12
TLQ 13-18
TLQ 19-24
3
2
1
0
1
0
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
April
May
June
July
1970
1971

Figure 24. Graph of temporal abundance of Asterias vulgaris in four TLQ blocks.

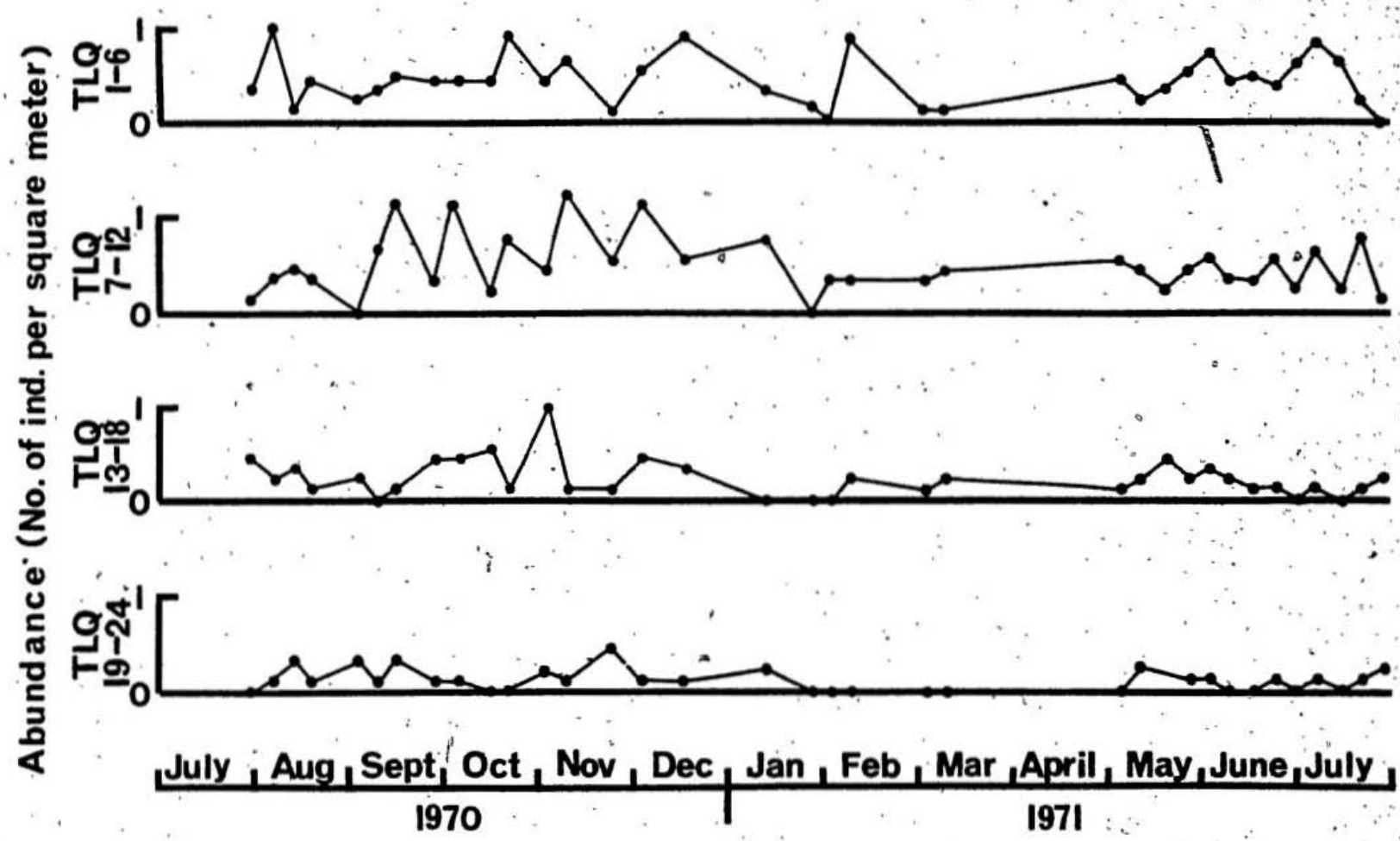
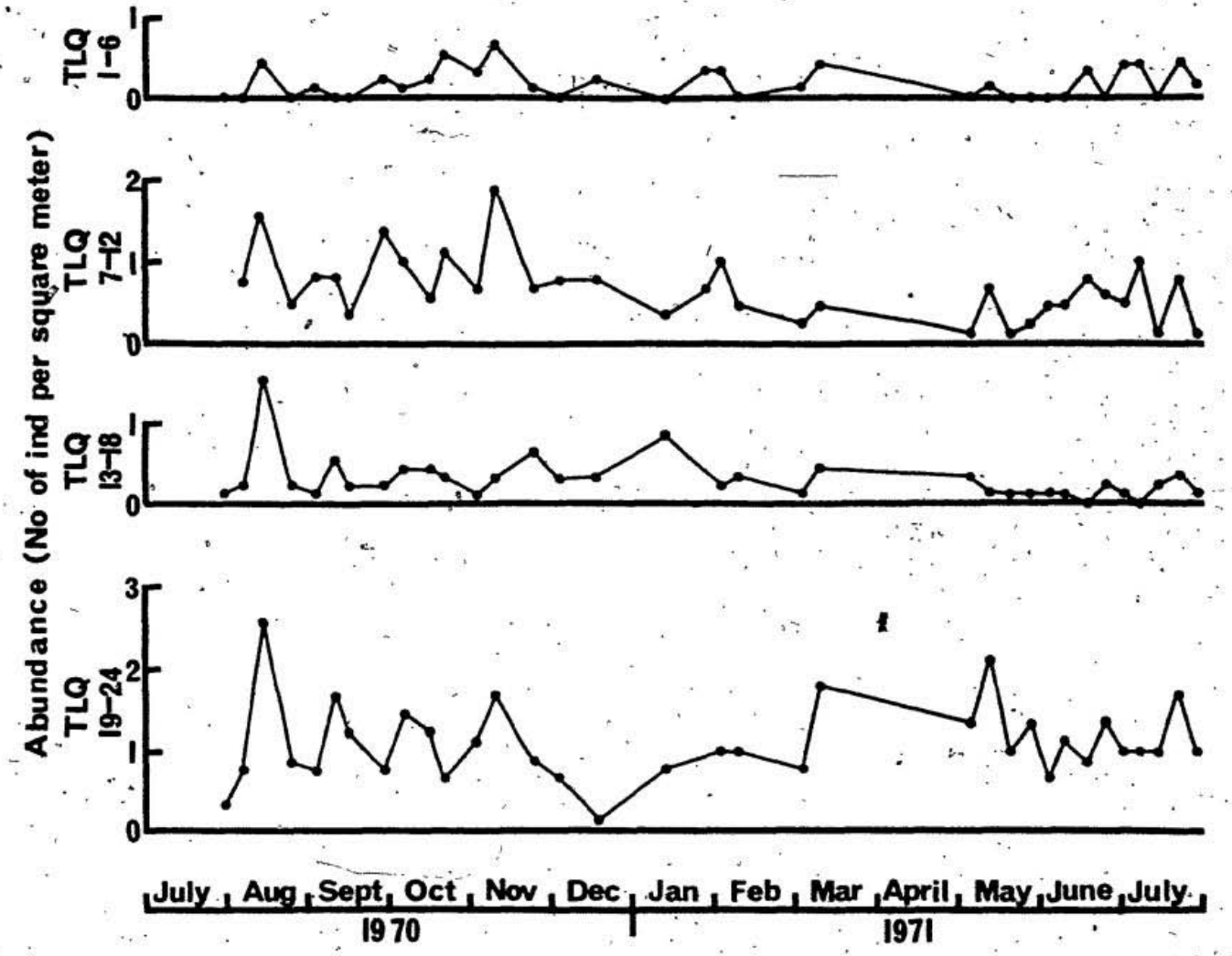

Abundance (No. of ind. per square meter)
TLQ 1-6
TLQ 7-12
TLQ 13-18
TLQ 19-24
0
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
April
May
June
July
1970
1971

Figure 25. Graph of temporal abundance of Henricia eschrichti in four TLQ blocks.


TLQ 1-6
TLQ 7-12
TLQ 13-18
TLQ 19-24
Abundance (No of ind per square meter)
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
April
May
June
July
1970
1971

4. Time periods characterized by short-term oscillations of equal amplitude can be interpreted as representing horizontal movements in and out of the sampled area, rather than emigration or immigration.[1]

5. Short term oscillating patterns in themselves indicate a non-uniform distribution of a species, possibly as a result of aggregation formation.[2]

6. Short-term adjacent oscillations of high and equal amplitude indicate a high locomotive activity of individuals of the particular species with a non-uniform distribution. Conversely, long period oscillations of low amplitude indicate uniform distribution, possibly with individuals demonstrating a low level of locomotive activity.

Leptasterias polaris

TLQ Block 1-6

In Table 7A, the major oscillations demonstrated by L.polaris in this block are listed giving maxima and minima. An examination of these data shows that maxima are high from August 24 to February 9, and lower until the end of the sampling period. A study of minima demonstrates that they built up to a peak on September 3, and had a slight decline until January 12. A sudden decrease occurred on February 2, with minima remaining low until the end of the sampling period. With maxima and minima considered together, then, a peak

---

[1] Vertical movement is not assumed, because significant changes in abundance would have been noted for TLQ blocks on either side of the affected TLQ block. Only L.polaris demonstrated temporal changes on TLQ blocks which were contingent. Mortality and natality would not affect repetitive short-term oscillation patterns in this manner.

[2] Aggregations are later considered in section I.

Table 7. Time periods of oscillations listing the maximal and minimal abundances (no. of individuals per square meter of unobscured bottom) of Leptasterias polaris for TLQ blocks 1-6 (A) and 7-12 (B).

A. Block 1-6

Oscillation No.	Minimum Value	Minimum Date	Maximum Value	Maximum Date
1	0.543	July 30, 1970	3.017	Aug. 24, 1970
2	1.419	Sept. 3	2.733	Oct. 15
3	1.261	Nov. 9	3.047	Nov. 23
4	1.020	Jan. 12, 1971	2.517	Jan. 26, 1971
5	0.334	Feb. 2	2.032	Feb. 9
6	0.569	March 2	1.477	March 9
7	0.478	May 19	1.464	July 14

B. Block 7-12

1	0.637	July 30, 1970	1.942	Aug. 24, 1970
2	0.803	Sept. 10	2.245	Oct. 5
3	0.667	Nov. 2	1.561	Dec. 1
4	0.669	Mar. 2, 1971	1.568	Mar. 9, 1971
5	0.571	June 3	1.296	June 24
6	0.238	July 1	0.930	July 28

abundance occurred beginning around August 24, and remained roughly constant until January 26 with low abundances prevailing thereafter until the end of the sampling period. These large abundance changes were possibly related to migration, natality, or mortality. As far as relationships between adjacent oscillations are concerned, the sampling year can be subdivided into three periods and are interpreted in Table 8.

TLQ Block 7-12

In Table 7B, the major oscillations demonstrated by L.polaris in this block are listed along with their maxima and minima. Minima rose from a low on July 20 to a peak on September 3, and demonstrated a slight decrease to January 12. From February 2 to May 19, minima are very low. Maxima demonstrate roughly the same relationship, with high maxima occurring on August 24, October 15, and November 23. A gradual decrease in abundance was progressively registered for maxima on January 26, February 9, March 9, and July 1. Hence, the pattern of temporal abundance when both maxima and minima are considered was as follows: abundance peaked during August through to October, then gradually decreased until the end of the sampling period. Based on oscillation characteristics the sampling year can be subdivided into four periods. The oscillation characteristics and the interpretation thereof are given in Table 9.

Asterias vulgaris

In Table 10, the oscillations demonstrated by A.vulgaris in TLQ block 7-12 are listed giving maxima and minima. In general, no clear pattern can be determined by examining these maxima and minima. However, two tendencies did appear evident. Minima are highest on

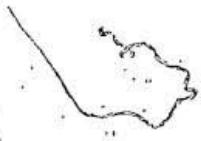


Table 8. Interpretation of oscillation characteristics as defined for specific periods of the year by the abundances of Leptasterias polaris in TLQ block 1 - 6.

Oscillation No's.	Period	Oscillation Characteristics	Interpretation
1,2	July 30, 1970 to Nov. 2, 1970	Two large, equal amplitude, long period oscillations.	1. Horizontal movement, i.e. between oscillations. 2. Major change in population dynamics to cause high abundances during this period.
3,4	Nov. 2, 1970 to Mar. 2, 1971	Two long period, moderate amplitude oscillations.	1. Slow increases and decreases in abundance. 2. Roughly uniform abundance.
5	Mar. 2, 1971 to June 3'71	Short period oscillation, moderately high amplitude.	1. Horizontal movement. 2. Non-uniform abundance.
6	June 3, 1971 to July 28'71	Incomplete.	1. Slow increase in abundance.

Table 9. Interpretation of oscillation characteristics as defined for specific periods of the year by the abundances of Leptasterias polaris in TLQ block 7 - 12.

Oscillation No's.	Period	Oscillation Characteristics	Interpretation
1 - 3	July 30, 1970 to Jan. 12, 1971	Two large amplitude, short period oscillations (1 & 3), with a long period, medium amplitude oscillation (2) in between.	1. #1 represents a major increase in abundance. 2. #2 reflects a high activity period with little overall change in abundance. 3. #3 represents high activity producing horizontal movements.
4,5	Jan. 12, 1971 to Mar. 2, 1971	Two, approximately equally large amplitude, short period oscillations.	1. Period of high activity producing horizontal movement. 2. Aggregation formation probably associated.
6,7	Mar. 2, 1971 to July 28, 1971	#6 is of long period, small amplitude. #7, incomplete, long period, small amplitude.	1. Roughly uniform abundance resulting from low activity and little aggregation formation.

Table 10. Time periods of oscillations listing the maximal and minimal abundances (no. of individuals per square meter of unobscured bottom) of Asterias vulgaris for TLQ block 7 - 12.

Oscillation No.	Minimum Value	Minimum Date	Maximum Value	Maximum Date
1	0.128	July 30, 1970	0.473	Aug. 13, 1970
2	0.000	Sept. 3	1.157	Sept. 15
3	0.338	Sept. 28	1.122	Oct. 5
4	0.223	Oct. 15	0.780	Oct. 20
5	0.445	Nov. 2	1.225	Nov. 9
6	0.556	Nov. 23	1.115	Dec. 3
7	0.557	Dec. 17	0.780	Jan. 12, 1971
8	0.000	Jan. 26, 1971	0.559	May 4
9	0.224	May 19	0.571	June 3
10	0.341	June 17	0.589	June 24
11	0.238	July 1	0.629	July 7
12	0.246	July 14	0.770	July 21
	0.116	July 28		

November 2, November 23, and December 17, and maxima are highest from September 15 to December 3. If the amplitude and period of the oscillations are examined, the sample year can be divided into two major divisions and one small period which are summarized in Table 11.

Since maxima and minima could not be effectively utilized to determine the temporal abundance patterns, these two major divisions, i.e. oscillations 2 - 7, and 8 - 12, were compared using a t- test of unpaired means (Wang programme). Period #2 having a mean abundance of 0.748 was found to be significantly different from period #3 (mean of 0.411) to the 0.005 critical level ($P(27, 3.525) = 0.998$). The period of July 30 to September 3 also has a low mean abundance of 0.388, and probably represented a continuation of the low abundance period of the previous year.

Henricia eschrichti

TLQ Block 7-12

In Table 12, the temporal oscillations demonstrated by H.eschrichti are listed giving maxima and minima. As was the case for A.vulgaris, no clear pattern is evident from an examination of these maxima and minima. Minima are highest on November 2 and November 23, and have an otherwise fluctuating pattern throughout the year. Similarly a peak in maxima occurred on November 9, with fluctuating abundances being higher from August 13 to November 9 and lower from December 17 to July 21. By means of an examination of the period and amplitude of oscillations, the sampling year can be roughly divided into three major periods. These periods are listed in Table 13 giving the characteristics and interpretation of each oscillation pattern.

Table 11. Interpretation of oscillation characteristics as defined for specific periods of the year by the abundances of Asterias vulgaris in TLQ block 7 - 12.

Oscillation No's.	Period	Oscillation Characteristics	Interpretation
1	July 30, 1970 to Sept. 3, 1970	Low amplitude, moderate period.	1. Horizontal movements.
2 - 7	Sept. 3, 1970 to Jan. 26, 1971	Large amplitude, short period oscillations.	1. High degree of activity and horizontal movement. 2. Aggregation formation.
8 - 12	Feb. 9, 1971 to July 28, 1971	One long period, small amplitude oscillation followed by a series of short period, small amplitude oscillations.	1. Period of low abundance characterized by low activity. 2. From May 4 to July 28, activity gradually increases, displaying increased horizontal movement.

Table 12. Time periods of oscillations listing the maximal and minimal abundances (no. of individuals per square meter of unobscured bottom) of Henricia eschrichti for TLQ block 7 - 12.

Oscillation No.	Minimum Value	Minimum Date	Maximum Value	Maximum Date
1	0.383	July 30, 1970	1.538	Aug. 13, 1970
2	0.485	Aug. 24	0.808	Sept. 3
3	0.347	Sept. 15	1.353	Sept 28
4	0.557	Oct. 15	1.114	Oct. 20
5	0.667	Nov. 2	1.893	Nov. 9
6	0.667	Nov. 23	0.778	Dec. 17
7	0.334	Jan. 12, 1971	1.003	Feb. 2, 1971
8	0.223	Mar. 2	0.448	Mar. 9
9	0.112	May 4	0.670	May 11
10	0.112	May 19	0.795	June 17
11	0.476	July 1	1.006	July 7
12	0.123	July 14	0.770	July 21
	0.116	July 28		

Table 13. Interpretation of oscillation characteristics as defined for specific periods of the year by the abundances of Henricia eschrichti in TLQ block 7 - 12.

Oscillation No's.	Period	Oscillation Characteristics	Interpretation
1 - 5	July 30, 1970 to Nov. 23, 1970	Large amplitude, short period oscillations.	1. Overall abundance remained roughly constant. 2. Considerable activity producing horizontal movements.
6 - 8	Nov. 23, 1970 to May 4, 1971	Small amplitude, long period oscillations.	1. Almost uniform distribution. 2. Gradual decrease in abundance. 3. Little horizontal movement because of low activity.
9 - 12	May 4, 1971 to July 28, 1971	Moderate amplitude, short period oscillations.	1. Abundance was roughly constant. 2. Activity resumed with horizontal movement.

In addition to the characteristic oscillation patterns of these three periods, their abundances were also characteristic. The mean abundance of period #1 (0.935) was much higher than the following periods (0.550 and 0.484 for periods #2 and #3, respectively). The t- test for unpaired means (Wang programme), was again utilized to test the significance of the differences between each pair of periods (Table 14A). These analyses showed that period #1 is significantly different from both periods #2 and #3, whereas, no significant differences existed between periods #2 and #3.

TLQ Block 19-24

The oscillation patterns demonstrated by H.eschrichti are listed in Table 15 giving maxima and minima. Again, no clear pattern of distribution could be discerned from an examination of the values of these maxima and minima. Throughout the sampling year, maxima and minima demonstrated an extremely fluctuating pattern with the highest minimum occurring on May 6, and the highest maximum on August 13. Using the time periods used for TLQ block 7-12, the year was subdivided into three periods based on oscillation characteristics. Table 16 lists the characteristics and interpretations of each period.

A series of unpaired t- tests was applied to each pair of periods to determine whether a significant difference existed between their mean abundances (1.162, 0.926 and 1.176 for periods #1, 2, and 3, respectively). Table 14B, a summary of these t- tests, shows that no significant differences did exist.

Table 14. Summary of analyses of mean abundances of Henricia eschrichti for three periods of the year (considered by pairs) using a t-test for unpaired means (Wang programme) for TLQ blocks 7 - 12 (A) and 19 - 24 (B).

* - significant to the 0.05 level

N.S. - not significant

A. TLQ Block 7 - 12

Period Pairs	Degrees of Freedom	t Value	Probability	Significance
1 & 2	20	2.291	0.967	*
1 & 3	23	2.638	0.985	*
2 & 3	20	0.510	0.384	N.S.

B. TLQ Block 19 - 24

1 & 2	20	1.024	0.682	N.S.
1 & 3	23	0.068	0.048	N.S.
2 & 3	20	1.351	0.807	N.S.

Table 15. Time periods of oscillations listing the maximal and minimal abundances (no. of individuals per square meter of unobscured bottom) of Henricia eschrichti for TLQ block 19 - 24.

Oscillation No.	Minimum Value	Minimum Date	Maximum Value	Maximum Date
1	0.333	July 30, 1970	2.556	Aug. 13, 1970
2	0.778	Sept. 3	1.667	Sept. 10
3	0.778	Sept. 28	1.444	Oct. 5
4	0.667	Oct. 20	1.667	Nov. 9
5	0.111	Dec. 17	1.000	Feb. 9, 1971
6	0.778	Mar. 2, 1971	1.778	Mar. 9
7	1.333	May 6	2.111	May 11
8	1.000	May 19	1.333	May 26
9	0.667	June 3	1.111	June 9
10	0.889	June 17	1.333	June 24
11	1.000	July 14	1.667	July 21
	1.000	July 28		

Table 16. Interpretation of oscillation characteristics as defined for specific periods of the year by the abundances of Henricia eschrichti in TLQ block 19 - 24.

Oscillation No's.	Period	Oscillation Characteristics	Interpretation
1 - 5	July 30, 1970 to Nov. 23, 1970	Large amplitude, short period.	1. Abundance in area remained roughly constant. 2. High activity producing pronounced horizontal movements.
6,7	Nov. 23, 1970 to May 6, 1971	Medium amplitude, long period.	1. Increasing abundance. 2. Little activity producing low degree of horizontal movement.
8 - 12	May 6, 1971 to July 28, 1971	Small amplitude, short period.	1. Roughly constant abundance. 2. Increased activity over period #2, producing some horizontal movement.

C-II.3 (iii) Summary and General Discussion of Temporal Distribution (Cliff Area)

In general, most of the temporal variation can be accounted for by horizontal movements[1] in and out of the sampled areas during periods of high locomotive activity of the particular species. Aggregation formation (discussed further in section I) may have accounted for extremely fluctuating values of the sampled populations during specific time periods.

It was apparent that other overall changes in abundance did take place during the sampling year. Such changes can be accounted for by the various processes of population dynamics which take place within a population to regulate its abundance or density. A simple model showing the interrelationship of mortality, natality, and migration, is presented in fig. 26 (adapted from Krebs, 1972). From this figure, it can be easily seen that immigration and natality increase population density, whereas, mortality and emigration decrease density.

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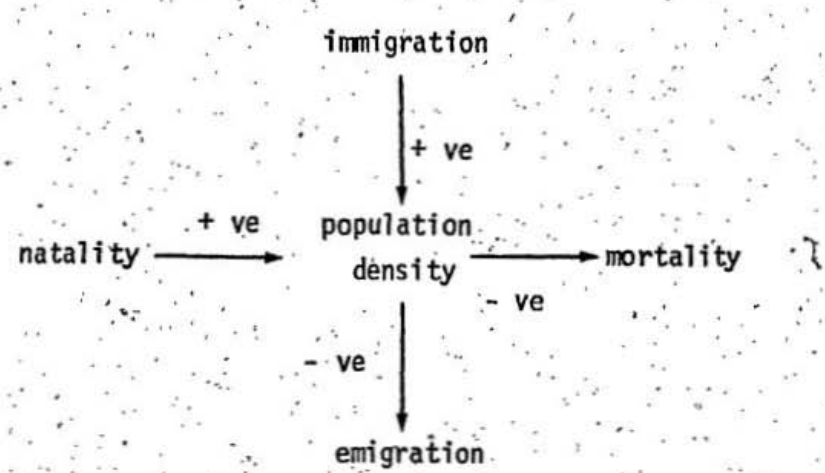
[1] A differentiation is made in this discussion between migration and horizontal movement in and out of the sampled area. Migration is used to refer to large scale movements of a population from one area to another; whereas horizontal movement refers to the random movement of sea stars in and out of the sampled area.

Figure 26. Model presenting the interrelationships of processes regulating population densities.


immigration
+ ve
natality
+ ve
population density
mortality
- ve
- ve
emigration

Changes in abundance may be caused by a single factor or a complex relationship involving changes in all factors. Since detailed studies were not performed to determine the rates of mortality, natality, and migration, over the year period, the exact causes of population fluctuations cannot be assessed.

C-III. Distribution of Asteroids in MAL Zone

C-III.1 Introduction

The MAL zone proved to be a difficult area to quantitatively sample for asteroid abundance. Reasons preventing a systematic survey of this zone were: a high degree of algal cover (preventing photographic sampling); a high degree of water disturbance (preventing a regular-interval sampling programme); and the non-uniformity of sea star distribution.

C-III.2 Materials & Methods

Methods for determining sea star abundance varied, depending on the temporal cycle of algal cover, water disturbance, and the parameter used to describe sea star distribution. Table 17 summarizes the sampling techniques, dates, and purpose of sampling.

C-III.3 Spatial Distribution C-III.3 (i) General Considerations

In the MAL zone, three species of sea stars were observed: two abundant species, L.polaris, and A.vulgaris, and a less abundant species H.eschrichti. Based on quantitative estimates of abundance (i.e. hand sample or photographic sampling techniques), the average abundance estimates of the three species were 6.000, 1.014 and 0.029 individuals per square meter of bottom for A.vulgaris, L.polaris and H.eschrichti, respectively.

Table 17. Outline of the sampling methods utilized to determine the distribution and abundance of asteroids found in the MAL zone.

Sampling Method	Description of Technique	Purpose	Dates
1. Photographic sampling technique	Temporary T.L. was run along bottom where no algal cover was present. Photographs, 1.5 X 1.0 meter, were taken along the T.L. every 1.5 m. Random photographs were also taken wherever algal density permitted unobstructed view of bottom. Photographs were analysed as outlined in section C-II.1(iii).	To determine the absolute and relative values of sea star abundances in areas not covered by algae.	Sept. 15, 1970 Oct. 19, 1970
2. Hand sample technique	1.0 X 1.5 meter rectangle from base of the photographic tower was moved along a temporary T.L. extending from cliff area T.L. in area of algal cover. Species, size, and numbers of sea stars were recorded.	To determine the absolute and relative abundances in areas covered by algae.	July 27, 1970 July 30, 1970 Aug. 9, 1970
3. Study of distribution with respect to mussel distribution.	Position of each L. polaris or A. vulgaris was recorded with respect to mussels. The three categories used in describing this distribution were: 1. Touching mussels, 2. Near mussels within 0.25 m. but not touching, and 3. Greater than 0.25 m. away from mussels.	To determine the effect of mussels on the distribution of L. polaris and A. vulgaris.	July 18, 1971
4. Study of distribution with respect to exposure.	Position and species were recorded with respect to the following exposure categories: 1. Exposed areas with no algae, 2. Exposed areas with algae, 3. Less exposed areas, and 4. Edge of plateau.	To determine the effect of exposure on distribution.	Dec., 1972
5. Stained sea star survey.	Number of individuals of each species collected for staining was recorded.	To determine the ratio of A. vulgaris to L. polaris.	Mar. 27, 1971
6. Feeding study.	Systematic swimming survey, with species and feeding data recorded for every encountered individual.	To determine the ratio of A. vulgaris to L. polaris.	May 13, 25, 1971 July 6, 27, 1971 Aug. 6, 1971

Spatial distribution of sea stars was non-uniform over the bottom of the MAL zone and appeared to be governed by two factors: distribution of mussels and distribution of protected areas. For studies involving distribution of sea stars with respect to these parameters, only L.polaris, and A.vulgaris were considered. Distribution of sea stars appeared to be affected to some degree by these factors at all times, but during the periods of least exposure, i.e. May to August, distribution of mussels appeared to be greater controlling factor which concentrated A.vulgaris and L.polaris abundance (Table 18). During the period of extreme exposure, September to December, sea stars were concentrated in areas of greatest protection (Table 19).

C-III.3 (ii) Distribution with Respect to Mussels (Table 18)

As stated in section B-IV.2(i), mussels covered approximately 50% of the bottom. ,Hence, if mussels had no apparent effect on distribution, the expected number of sea stars in contact or near mussels would represent approximately 50% of the total number of sea stars. Since only 22.1% (L.polaris) and 5.6% (A.vulgaris) of each population were found at distances greater than 0.25 m from a mussel, the mussels appeared to have a strong influence on the distribution of these predators. Also evident is that mussel distribution had a greater effect on the distribution of A.vulgaris than on L.polaris, the percentage of the population displaying contact with mussels being much greater for A.vulgaris. The habit of L. polaris of resting near but not on mussels is shown by the high percentage of individuals in category 2 (also see fig. 27).

Table 18. Positions of Leptasterias polaris and Asterias vulgaris with respect to Mytilus edulis in the MAL zone.

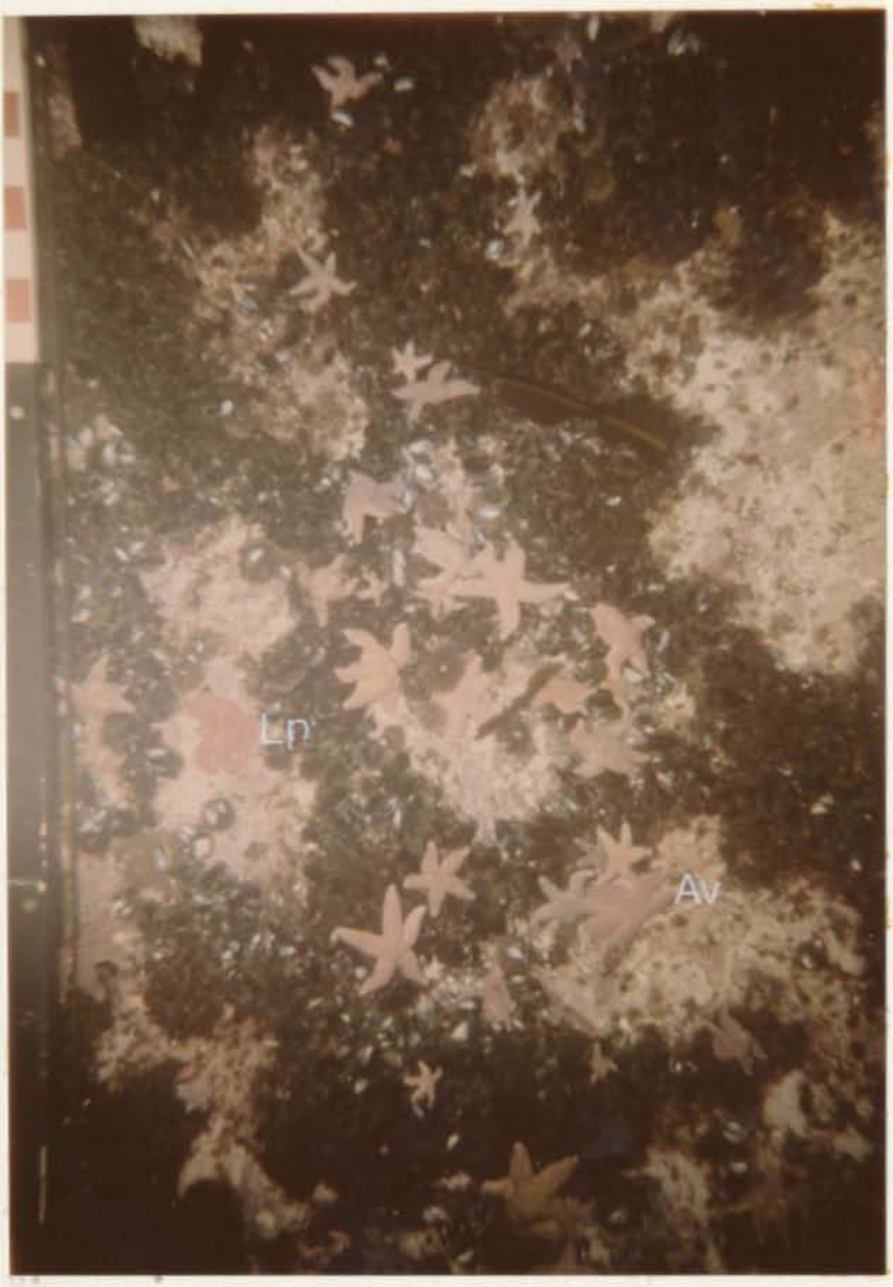
Position of Sea Star With Respect to Mussels	Leptasterias polaris			Asterias vulgaris		
	Number	% of Total		Number	% of Total	
1. In contact with at least one mussel.	27	39.7		56	78.9	
2. No contact with a mussel, but less than 0.25 m. away from a mussel.	26	38.2	77.9	11	15.5	94.4
3. Not within 0.25 m. of a mussel.	15	22.1		4	5.6	

Table.19. Positions of Leptasterias polaris and Asterias vulgaris with respect to exposure in the MAL zone.

Exposure	Leptasterias polaris		Asterias vulgaris	
	Number	% of Total	Number	% of Total
1. Exposed areas with no algae.	2	3.7	0	0.0
2. Exposed areas with algae.	7	13.0	0	0.0
3. Less exposed areas, eg. cracks, hollows, troughs, etc.	12	22.2	8	47.1
4. Edge of plateau.	33	61.1	9	52.9

Figure 27. Underwater photograph taken in the MAL zone showing positional relationships of Asterias vulgaris, Leptasterias polaris, and Mytilus edulis.

Note the position of Leptasterias polaris (Lp) on the rock substrate, and aggregations of Asterias vulgaris (Av) on Mytilus edulis.


Lp
Av

C-III.3(iii) Distribution with Respect to Exposure

In Table 19, the percentages of the populations of A. vulgaris and L. polaris are listed in decreasing order of exposure, i.e. categories 1 to 4. As can be seen, the percentages of the populations were largest in areas of least exposure and smallest in exposed areas. Although no estimate was made of the percentages that each category represented of the bottom, it was clear that categories 1 and 2 (exposed areas), comprised a much larger percentage of the surveyed area than categories 3 and 4 (unexposed areas). Hence, the concentrations of each species in areas of protection are highly significant. L. polaris demonstrated a greater tendency in habitation of areas of exposure than did A. vulgaris, having 16.7% of the population in areas of extreme exposure, whereas no A. vulgaris (0%) were observed in areas of this degree of exposure.

C-III.3(iv) Combined Effect of Exposure and Mussel Distribution

In the two previous studies, each factor was examined individually, controlling for the other factor. The periods of the year during which each survey was undertaken were carefully selected to demonstrate the greatest effect of the parameter studied. Intermediate distribution patterns showing the combined effect of these parameters were assumed but not tested. Several general observations, however, indicate the validity of this hypothesis. Greatest abundances of both species were found in areas of protection where there were large concentrations of mussels. Mussel beds, located in areas which offered no or little protection from water disturbance, were only populated by sea stars during extended periods of calm. Some mussel beds in a perpetual

condition of water disturbance, ie. at the base of Mad Rock, were never populated by sea stars. Hence, temporal changes in feeding rate and exposure both affected the spatial distribution of sea stars in the MAL zone.

C-III.4. Temporal Changes in Absolute and Relative Abundances of L.polaris and A.vulgaris in the MAL Zone.

As we have seen in the three previous sections, A.vulgaris and L.polaris demonstrated a degree of interspecific variation in their spatial distribution. A.vulgaris had a greater tendency to aggregate in areas of mussels and protection than did L.polaris. In Table 20, the relative and absolute abundances of A.vulgaris and L.polaris are listed for various times of the year. The significance of these changing RA values is difficult to justify because of the varied nature of the sampling techniques and area sampled during each survey. Although trends in RA values of these species appear to be clear from these data, these trends may simply be a result of changes in sampling technique which might favour the distribution of one of the species over the other at a specific sampling date. For this reason, it is felt that an analysis of these changing RA values would be meaningless.

Table 20. Relative and absolute abundance estimates of Asterias vulgaris and Leptasterias polaris in the MAL zone.

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[1] Edge of the plateau and MAL zone together.

[2] Shows the effect of redistribution of sea stars after the stained sea star study.

* Calculation includes consideration of unknown sea stars.

Date	No. Individuals of *A. vulgaris*	No. Individuals of *L. polaris*	Total No. of Individuals	R.A. of *A. vulgaris*	R.A. of *L. polaris*	No. of Samples	No. Individuals of *A. vulgaris* per 1.5 m^2	No. Individuals of *L. polaris* per 1.5 m^2	Method
July 27, 31, 1970	29	8	37	78.4	21.6	8	3.625	1.000	hand sample
Aug. 9, 1970	13	9	22	59.1	40.9	3	4.333	3.000	hand sample
Sept. 15, 1970	70	10	80	87.5	12.5	5	14.000	2.000	photography
Oct. 19, 1970	95	8	103	92.2	7.8	7	17.254*	1.460*	photography
[1] Mar. 27, 1971	154	124	278	54.4	44.6	-	--	--	stained sea star study
[2] May 13, 25, 1971	13	14	27	48.1	51.9	-	--	--	predation study
July 6, 22, 1971	149	52	201	74.1	25.9	-	--	--	predation study
Aug. 6, 1971	82	45	127	64.4	35.4	-	--	--	predation study

D. Migration and Movement Studies

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D Migration and Movement Studies

D-I Introduction

Two studies were undertaken to determine the degree of migration and movement demonstrated by three asteroid species. Since the population abundance of S.endeca was too low to assess from the photographic analysis, a study of its movements was undertaken to determine its distribution and activity in the cliff area.

In the second study, L.polaris and A.vulgaris collected in the MAL zone were stained and released again in the MAL zone to determine the extent of emigration of these species from this area.

D.II Study of the Movements of Two Specimens of Solaster endeca

D-II.1 Materials and Methods

Two specimens found in area E in the spring of 1970 were observed to determine the degree, direction and character of movement which they underwent in their natural environment. The first method (employed from June 8 to June 17) consisted of measuring the distance between each specimen[1] and a fixed point. A piton was hammered into a crevice near the location of both specimens and the distances of each specimen from the piton were marked by tying a knot in a length of an almost

---

[1] Throughout the duration of these studies, no other S.endeca specimens were observed in this area; hence, confusion with other S.endeca individuals did not arise. Specimen #2 could be recognized immediately from specimen #1 because one of its arms was considerably shorter than the others, whereas the arms of specimen A were of equal length. Colouration of both specimens was also different. Specimen #1 was an orange-purple, while specimen #2 was a deep purple. Also specimen #2 could be recognized by a circular band of discolouration on the aboral surface near the circumference of the central disc.

unstretchable cord at the location of the asteroids. For this procedure, one diver held the metal end of the measuring cord tight against the piton, while the other diver unravelled the rope from the spool, pulled the rope taut, and tied a knot in the rope at a point indicating the centre of the central disc of each specimen.

From June 17 to October 17, sampling was performed on a regular weekly basis using the TL as a frame of reference. A piece of rope was tied to the TL to indicate the origin for a Cartesian coordinate system with the TL serving as the Y axis. After locating a specimen, diver A, holding the free end of the measuring cord over the central disc of the specimen, motioned to diver B to slide the metal right angle along the TL until the measuring line was perpendicular to the TL. A knot was placed on the taut line at the centre of the central disc of the specimen indicating the X coordinate of its position. With diver B holding the metal right angle firmly fixed, diver A swam to the origin and tied a knot in the taut measuring line, indicating the Y coordinate of the specimen's location. To prevent confusion, a double knot was placed on the Y coordinate. The X and Y coordinates were measured to the nearest 5 cms. in the laboratory using a 100 meter tape. Owing to the slight elasticity of the measuring line, measurements were taken at the point when the rope was just pulled straight, but not under stress.

From October 17, 1970 to July 14, 1971, diving time did not allow this experiment to be carried out on a regular basis. However, whenever either of these specimens was observed, its approximate

position was recorded without the benefit of use of the afore-described quantitative procedures. Also some measurements were taken from the transect photographic series when possible.

D-II.2 Results and Discussion

On figs. 28 and 29, the positions recorded for the two individuals of S.endeca have been plotted and joined by arrows in order to visualize the minimum path each individual might have taken between sampling dates. The exact path and activity of each sea star cannot be determined without continuous observation. However, by studying the amount of displacement between sample dates, correlated with other observations of activity of these specimens, some tentative conclusions can be made concerning their activity and movements.

1. Except for the period A, which is noted for both specimens, and B, for specimen #1, both individuals appeared to be confined to a small area of the bottom, having a depth range of 24-31 meters. The area enclosing the observed positions (excluding times A and B) was approximately 5 X 7 meters for specimen #1 and 5 X 10 meters for specimen #2.

2. During period A (October 17 - February 20), both specimens were observed in area D; however, their exact locations were not measured.[1] Specimen #1 also moved from this area during the period B, when it moved out onto the sand bottom and captured a Cucumaria frondosa. These observations are reported in section E-III.3. After February 20,

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[1] Restricted diving time during this period necessitated a decreased emphasis on this study.

Figure 28. Plot of movements exhibited by a single specimen (#1) of Solaster endeca. Axes in meters. (See the text for description of A and B).

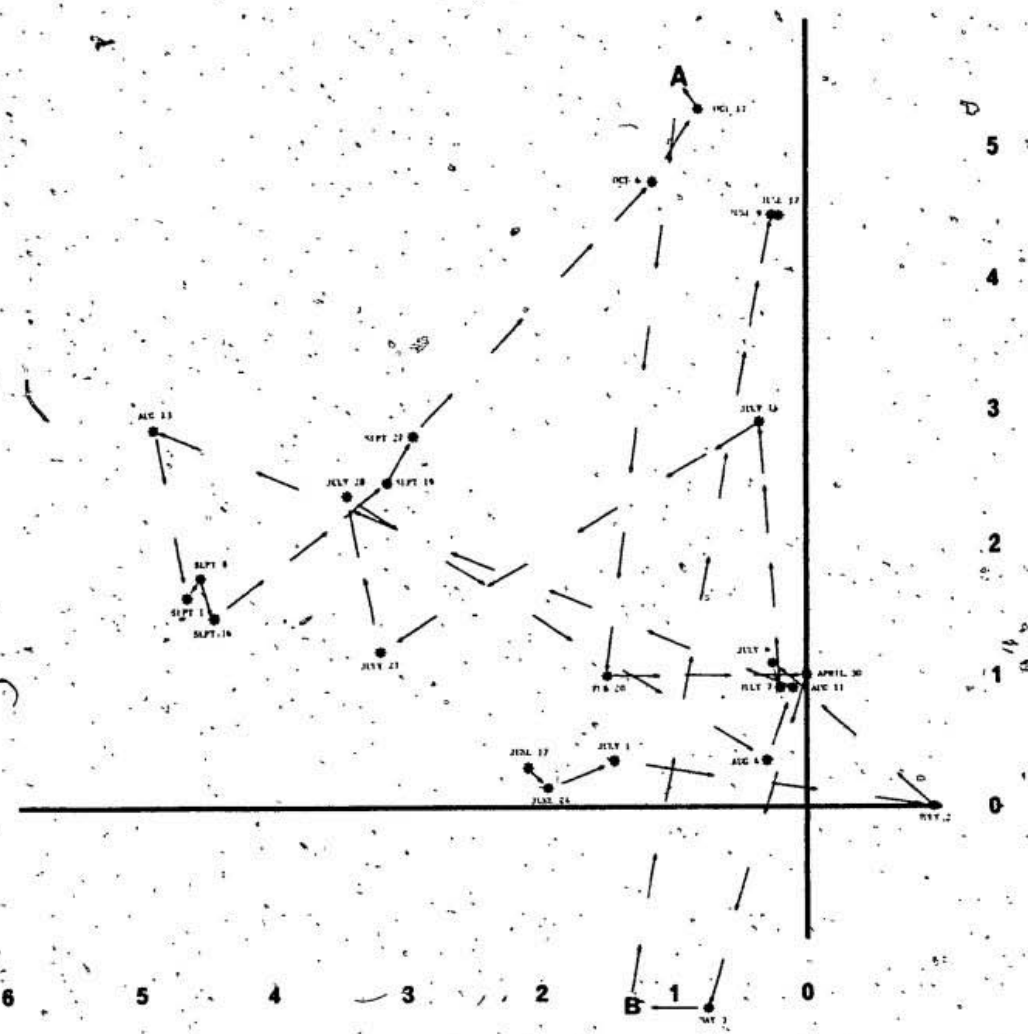
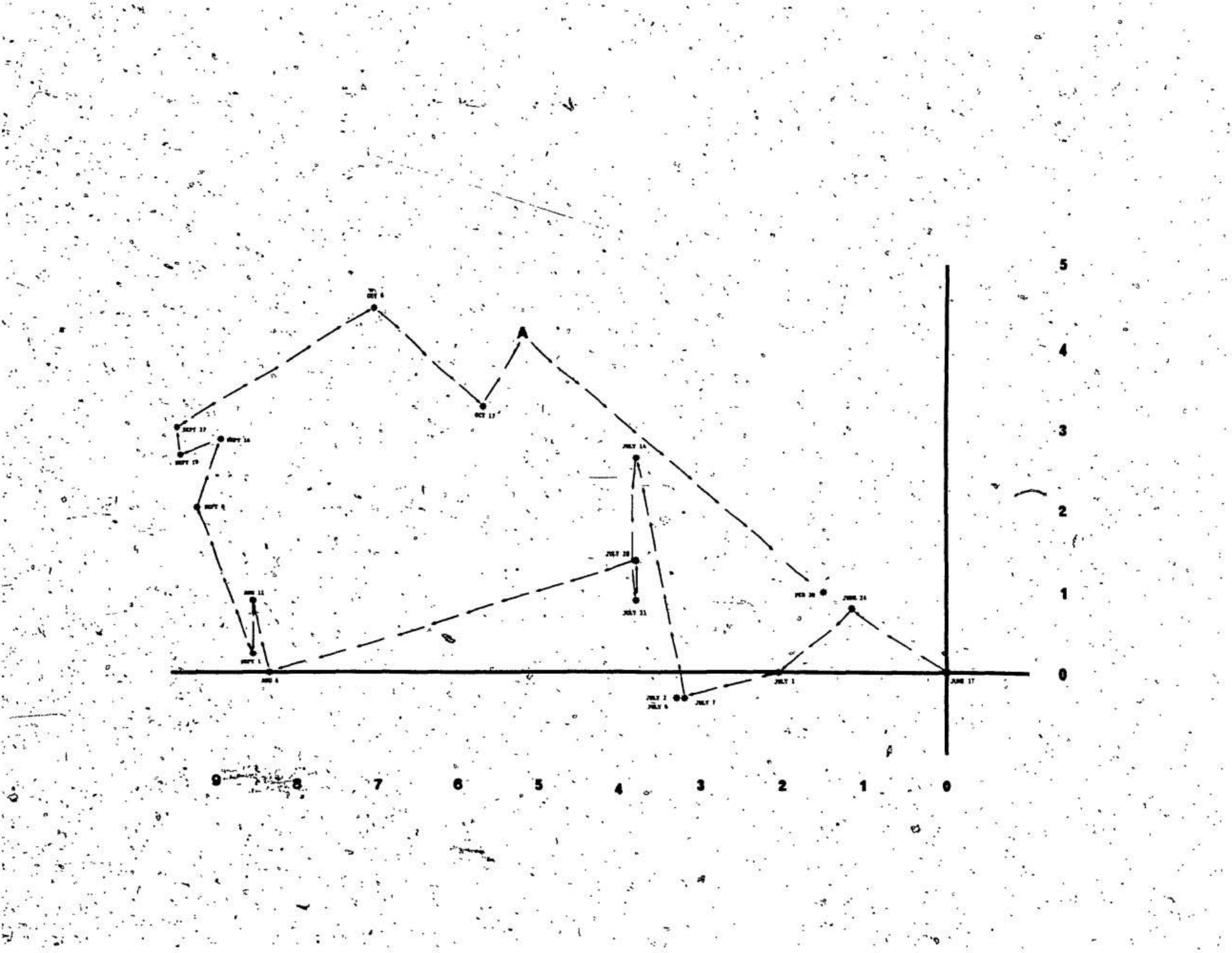

A
B
5
4
3
2
1
0
8
7
6
5
4
3
2
1
0

Figure 29. Plot of movements exhibited by a single specimen (#2) of Solaster endeca. Axes in meters.

(See text for description of A.)


A
5
4
3
2
1
0
9
8
7
6
5
4
3
2
1
0

specimen #2 moved out of this area, moving seaward (to the left of the graph) along the sand-rock border.

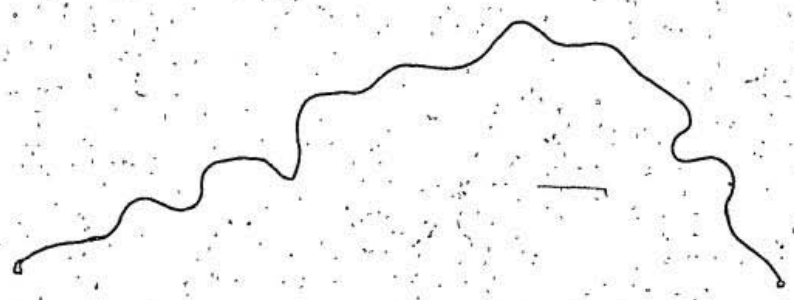
If we consider that close proximity of positions on consecutive dates indicate little movement or activity, and large displacement on consecutive dates indicates periods of high activity, we see an activity pattern that appears to be related to feeding. Movements appear to be random, suggesting a food foraging strategy with periods of high activity often followed by periods of low activity. As will be seen in section E-III.3, prey capture, ingestion, and digestion of sea cucumbers may take as long as fourteen days, and during this period, the sea star undergoes little movement. Using these two factors (ie. displacement and prior knowledge of feeding behaviour), one can speculate on the major activity which the sea stars underwent between sample dates. Since the interval between sampling dates was large (usually seven days), the exact dates on which feeding and digestion began or ended cannot be determined. Hence Table 21, an analysis of the major activity taking place during sampling intervals for the period June 17 to October 17, does not clearly define the temporal boundaries of the activities of these sea stars, but refers only to what might have occurred between sampling dates.

D-III Study of Movements of Stained Sea Stars

D-III.1 Materials and Methods

A total of 124 Leptasterias polaris and 154 Asterias vulgaris, collected by divers on March 27, 1971 from the algal plateau, were stained onboard a dory, and returned immediately to their former positions. Staining was accomplished by suspending batches of 20-40

Table 21. Speculation of the major activities displayed by two specimens of Solaster endeca during movement studies.



Specimen No. 1		Specimen No. 2	
Sampling Date Intervals	Major Activity	Sampling Date Intervals	Major Activity
June 17 - July 1, 1970	feeding	June 17 - July 1, 1970	foraging
July 1 - July 21	foraging	July 1 - July 7	feeding
July 21 - July 28	feeding	July 7 - July 21	foraging
July 28 - Aug. 4	foraging	July 21 - July 28	feeding
Aug. 4 - Aug. 11	feeding	July 28 - Aug. 4	foraging
Aug. 11 - Sept. 1	foraging	Aug. 4 - Sept. 1	feeding
Sept. 1 - Sept. 16	feeding	Sept. 1 - Sept. 16	foraging
Sept. 16 - Sept. 19	foraging	Sept. 16 - Sept. 27	feeding
Sept. 19 - Sept. 27	feeding	Sept. 27 - Oct. 6	foraging
Sept. 27 - Oct. 6	foraging	Oct. 6 - Oct. 17	feeding
Oct. 6 - Oct. 17	feeding		

specimens, enclosed in a burlap sack, in a well aerated solution of Nile Blue Sulphate (concentration: 1 gm. Nile Blue Sulphate per 1 liter of sea water (Feder, 1955)). The water soluble vital dye was procured from the National Analine Company.

Records were kept by divers of any stained specimens observed during each of the following procedures:

(i) Field Feeding Study

The position of the observed stained sea star was recorded assigning it to one of the major divisions of the cliff (ie. areas B, C, D or E) called predation areas for the field feeding study.[1]

(ii) By Use of Horizontal Transect (H.T.)

A 10 meter length of rope (same type as TL), marked at the midpoint and weighted with lead, was placed by divers at right angles to the TL with the mid-point on TLQ #1. Divers using clip boards with Cronaflex sheets for recording, and 1.5 meter sticks for reference, swam adjacent to the HT., in opposing directions on opposite sides of the HT. Hence, recordings were made of the species of all observed sea stars found on a 1.5 meter strip on each adjacent side of the 10 meter HT. When divers reached the end of the H.T., the line was lifted, repositioned in a similar manner at TLQ #3, and the observation - recording procedure repeated. H.T. series were carried out twice, on June 22, 1971 (TLQ #'s 1-5), and on July 20, 1971 (TLQ #'s 1-10).

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[1] Areas B,C,D and E are subsets of the larger predation areas, defined in section E-II.1 (fig. 30). Areas B, C, D, and E refer to the areas in the immediate vicinity of the TL, whereas, predation areas (B, C,D and E) refer to horizontal extensions of these areas on either side of the TL to the boundaries of the study area.

D-III.2 Results and Discussion

D-III.2 (i) Observations from Field Feeding Study

Of the 278 sea stars stained and released, a relatively small number of stained sea stars were observed to have moved from the MAL zone into the Cliff Area. Most of these observations (ie. 22 of 24 for L.polaris and 21 of 23 for A.vulgaris)[1] were made in P.A.B. indicating a very limited degree of movement of the MAL zone sea stars. Although the populations appear to be somewhat restricted in their movements, some individuals were observed to achieve large displacements from their original location. On May 31, 1971, two L.polaris were observed a great distance from the original release site. One was observed near TLQ 14, ie. 20±5 meters from its original location, a movement which took a maximum of 65 days. Similarly, the other individual was observed in P.A.D. August 11, also indicating a minimum movement of 20 ± 5 meters in a maximum period of 129 days.

D-III.2 (ii) Horizontal Transect Survey

During the first sampling survey, only one of a total of 28 A.vulgaris specimens observed was stained. None of the 27 L.polaris were stained. Similarly in the 10 X 15 meter (TLQ's 1-10) block examined on July 22, four stained A.vulgaris were observed of the total of 64, and none of the 62 L.polaris observed were stained. These results appear to indicate that some degree of movement by A.vulgaris from the MAL zone does exist; however, only a small percentage

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[1] Note that the large number of recordings of stained sea stars in the cliff area results from repetitive observations, such that the same individual may be observed on different sampling dates. A maximum of 8 stained A.vulgaris and 6 stained L.polaris were observed on any one sample date.

of the total population of an area can be considered migratory during the time period April - July. Downward movement by L.polaris was negligible according to this survey, since no stained L.polaris were observed in this zone.

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E. Feeding Studies

E-I Introduction

Prey, prey selectivity, and rate of feeding have long been considered important factors, not only in studies of the basic biology of asteroids, but also in studies relating distribution of a species to its feeding habits. A tabular review of asteroid species, location, prey, and references is provided in Feder and Christensen (1966). Few of these researchers have concentrated efforts on the species which are endemic to the shallow waters of Newfoundland. Of these studies, no reference is made to the feeding biology of the asteroids as it occurs in the present study area. For these reasons, an extensive study of the prey, feeding habits, prey preference, and rate of feeding of the sea stars of the study area was undertaken to fill the void in our knowledge of the basic biology of Newfoundland sea stars.

A consideration of the relationships of aspects of the feeding biology of these sea stars to spatial distribution and feeding niche is also presented. Field observations of feeding, coupled with laboratory prey preference experiments were utilized to elucidate these study parameters.

E-II Field Observations

E-II.1 Materials and Methods

Two series of field predation studies were completed: a preliminary study (from September to November 1970) and a detailed study (from May to August, 1971). In the preliminary study, all

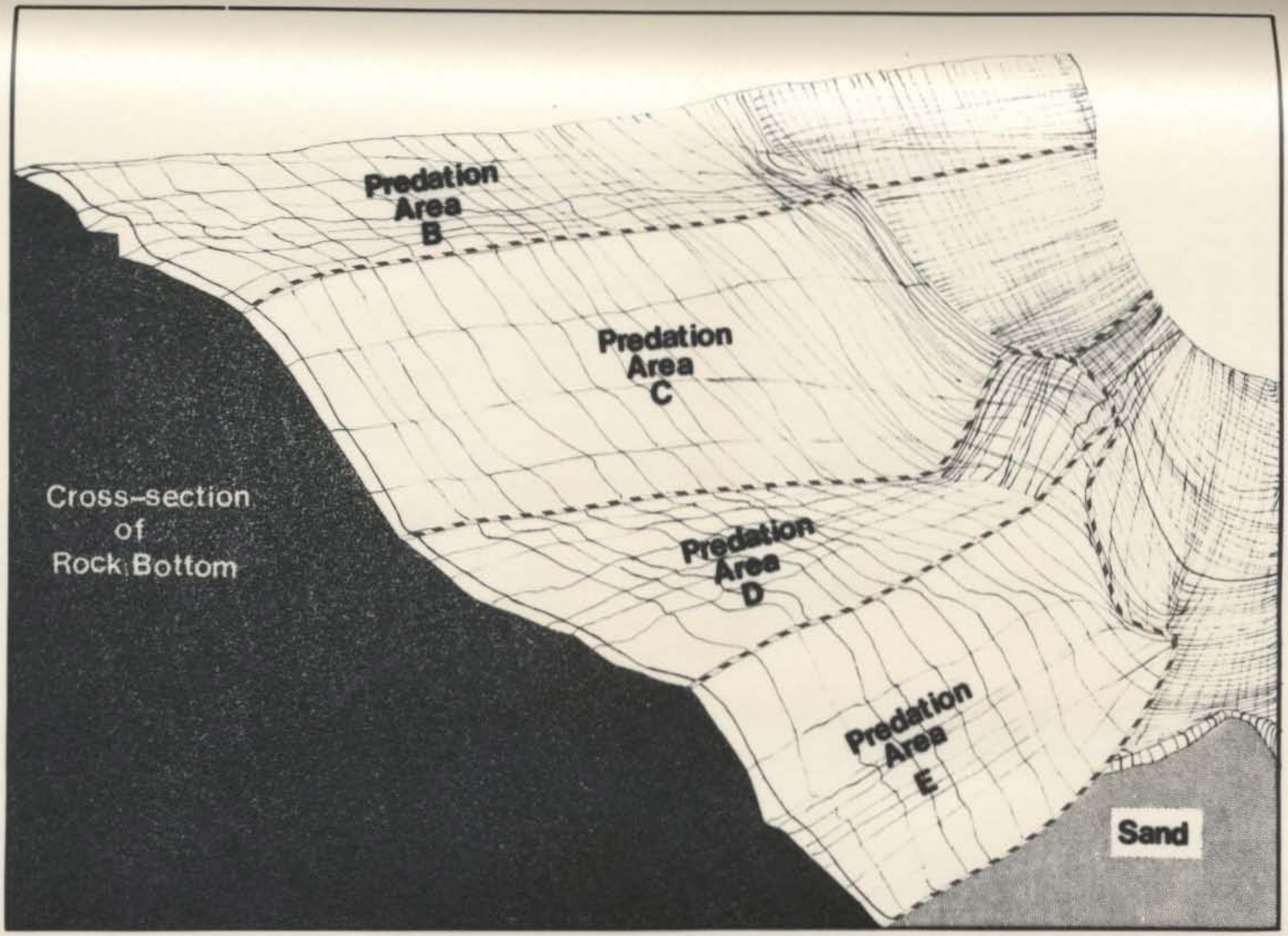
observed sea stars in the study area were turned over, examined for feeding activity, and returned to their original position on the bottom. A sea star was considered to be feeding if its cardiac stomach was everted, in the case of L.polaris, A.vulgaris, and C.papposus, or if prey was observed to be at least partially enclosed by the mouth, in the case of S.endeca. A record was made of the species of each feeding sea star and the species of its prey on Crona-flex drafting film.

For the detailed predation study, the study area was divided into five predation areas (P.A.'s A through E) on the basis of depth and slope (fig. 30). Each area (except P.A. A) was approximately 9 meters wide and extended for about 50 meters on either side of the TL. Predation area A was the entire MAL Zone and had an approximate area of 600 square meters.

Using the same method as in the preliminary study, the detailed predation study was carried out on one or two P.A.'s per dive and the results for each P.A. were recorded separately. The following information for the detailed study was recorded on Crona-flex drafting for each observed sea star: the date of observation, presence or absence of feeding, and the species of any observed prey. Six dives were made during the period of study for each P.A. in the following sequence: 1. P.A. E, 2. P.A.'s C & D, and 3. P.A.'s A & B.

All observations and recordings were made by the author while the diving partner surveyed the P.A. for sea stars for the author to observe.

Figure 30. Three dimensional drawing of the Cliff area defining predation areas.


Predation
Area
B
Predation
Area
C
Predation
Area
D
Predation
Area
E
Cross-section
of
Rock Bottom
Sand

E-II.2 Preliminary Study

Leptasterias polaris

Only feeding individuals of this species were recorded; hence, no determination of the percentage of population feeding could be made. Most (14) of the observations were made in P.A.'s D and E, and the remaining (6) were made in P.A. B. In both areas, Mytilus edulis was its major prey representing 83.3% of the total in P.A. B, and 64.3% of the combined total for P.A.'s D and E. Only one other prey item was noted in P.A. B, Thais lapillus; representing the remaining 16.7%; whereas in areas D and E, three other prey species were noted: Volsella modiolis (14.3%), Hyas araneus (7.1%), and Strongylocentrotus droebachiensis (7.1%). The prey of one (7.1%) feeding sea star could not be determined.

Asterias vulgaris

Again no data on feeding percentages could be determined because the number of non-feeding individuals was not recorded. In P.A. C, two individuals were observed feeding on M.edulis (66.7%) and one individual was observed feeding on Hyas araneus (33.3%). In the P.A.'s D and E, four individuals were observed feeding, all upon M.edulis (100%).

Crossaster papposus

A total of 28 C.papposus individuals was examined of which 18 were found to be feeding (for a percentage of 64.3%). All observed specimens of this species were located in P.A.'s D and E. During the time period of this experimental series, sea stars were the largest single component, representing 33.3% of its total prey. All

sea stars, observed being fed upon, were either A.vulgaris or L.polaris, although the proportion of each species could not be determined because of early difficulties in identification of partially digested sea stars.

Apart from one sighting of C.papposus (5.6%) feeding upon a bryozoan, all remaining identifiable prey belonged to the phylum Cnidaria with Gersemia sp., Metridium senile, and an unidentifiable hydroid representing 16.7%, 11.1% and 5.6% of its diet respectively. Prey which could not be identified accounted for the remaining 22.1% of the feeding observations.

E-II.3 Detailed Feeding Study

E-II.3 (i) Leptasterias polaris

E-II.3 (ia) Percentage of Population Feeding (Fig. 31)

A total of 665 individuals were examined during this study for P.A.'s A through E. Of this total only 127 were feeding, resulting in an average feeding percentage of 19.1. Values of feeding percentage, however, were not constant over the five P.A.'s (Fig. 31). In P.A.'s with steeper slopes (C & E), low percentages of the population were observed feeding (9.2% and 4.4%, respectively); whereas, much higher percentages were observed feeding in areas of more gentle slope (P.A.'s A, B, and D).

Also apparent was a general decrease in feeding percentage with increasing depth (ie. from P.A. A to P.A. E).

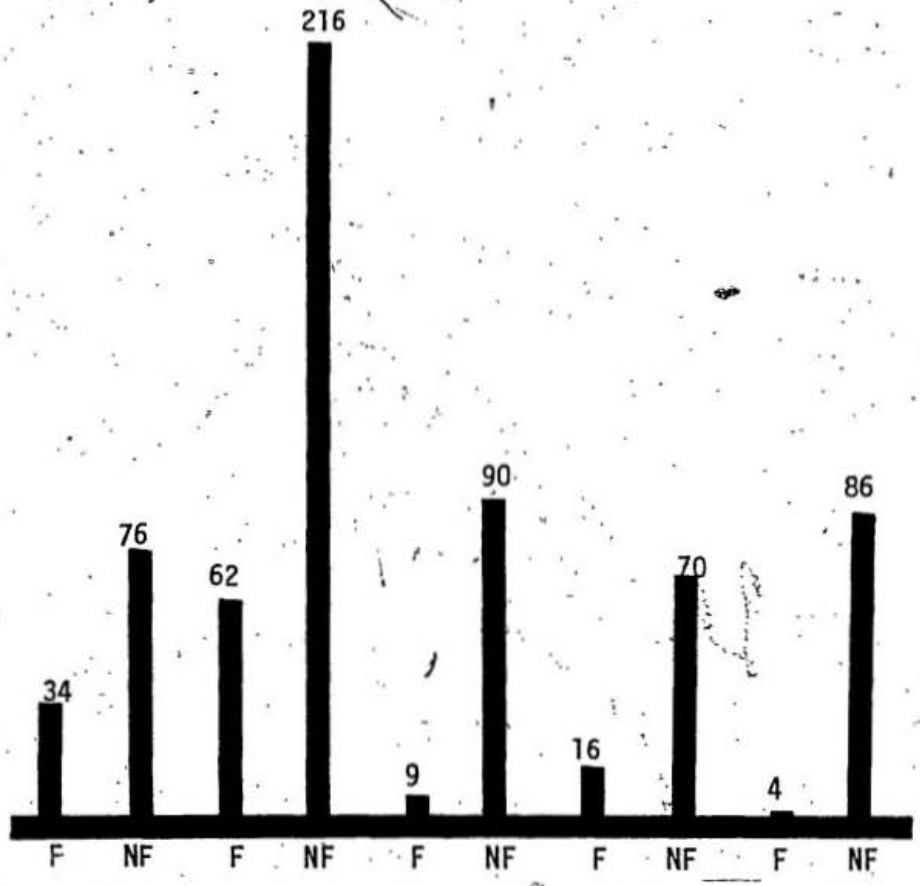
E-II.3 (ib) Prey Selectivity (Table 22)

Leptasterias were observed feeding on 12 different species.

Figure 31. Relative numbers of feeding and non-feeding individuals and percentage of the population feeding of Leptasterias polaris in the five predation areas studied in Logy Bay.

F - feeding

NF - non-feeding



Percentage of Population Feeding	30.9	22.9	9.1	18.6	4.4
Area	A	B	C	D	E

Table 22. Summary of the detailed feeding study of Leptasterias polaris listing prey species and the percentage each prey species represented of the total prey for each predation area.

Figures in brackets are the numbers of observations of feeding on the prey species.

Prey Species	Predation Area					Total
	A	B	C	D	E	
Mytilus edulis	88.2 (30)	72.6 (45)	11.1 (1)	-	-	60.8 (76)
unknown	-	6.5 (4)	22.2 (2)	37.5 (6)	-	9.6 (12)
Hiatella arctica	5.9 (2)	3.2 (2)	44.4 (4)	12.5 (2)	25.0 (1)	8.8 (11)
Thais lapillus	5.9 (2)	8.1 (5)	-	6.3 (1)	-	6.4 (8)
Mallotus villosus (Muller)	-	6.5 (4)	-	-	25.0 (1)	4.0 (5)
Tonicella marmorea	-	-	11.1 (1)	18.75 (3)	-	3.2 (4)
Buccinum undatum	-	1.6 (1)	-	6.3 (1)	-	1.6 (2)
Musculus discors L.	-	-	-	-	50.0 (2)	1.6 (2)
Acmaea testudinalis	-	-	11.1 (1)	-	-	0.8 (1)
Balanus balanus (L.)	-	1.6 (1)	-	-	-	0.8 (1)
Anomia aculeata	-	-	-	6.3 (1)	-	0.8 (1)
Margaretes costalis	-	-	-	6.3 (1)	-	0.8 (1)
Lacuna vincta	-	-	-	6.3 (1)	-	0.8 (1)

over the entire study area. Its dominant prey was clearly Mytilus edulis in areas of high abundance of this bivalve, i.e. P.A.'s A and B. In areas of sparse M.edulis abundance (P.A.'s C, D, and E), predation of this bivalve is limited (only one observation).

In all P.A's, Hiatella arctica was observed to have been preyed upon. Hence even in areas of high M.edulis abundance, H.arctica was selected to some extent as food. The area of greatest H.arctica predation was P.A. C, i.e. the first region deeper than the zone of high M.edulis abundance.

Ranking third in total number of individuals eaten over the entire study area was Thais lapillus. In the shallower P.A.'s (A and B), where this species was abundant, seven feeding observations were made. In P.A.'s C through E where T. lapillus had a sparse distribution, only one individual was observed being fed upon.

Of the remaining prey species, only two species were non-molluscan, the barnacle Balanus balanus (L.) and moribund caplin (Mallotus villosus) (Muller). Hence, molluscs represented 10 of the 12 prey species of L.polaris.

E-II.3 (ii) Asterias vulgaris

E-II.3 (iia) Percentage of Population Feeding (Fig. 32).

During the detailed field feeding study, 693 A.vulgaris were examined of which 223 were feeding, yielding an average feeding percentage of 32.2. A. vulgaris in P.A. B had the highest feeding percentage with 41.2% of the sampled population feeding. A decrease in feeding percentage with increased depth was noted for P.A's C, D and E. The slope of the P.A. appeared to have little or no effect on the feeding rate.

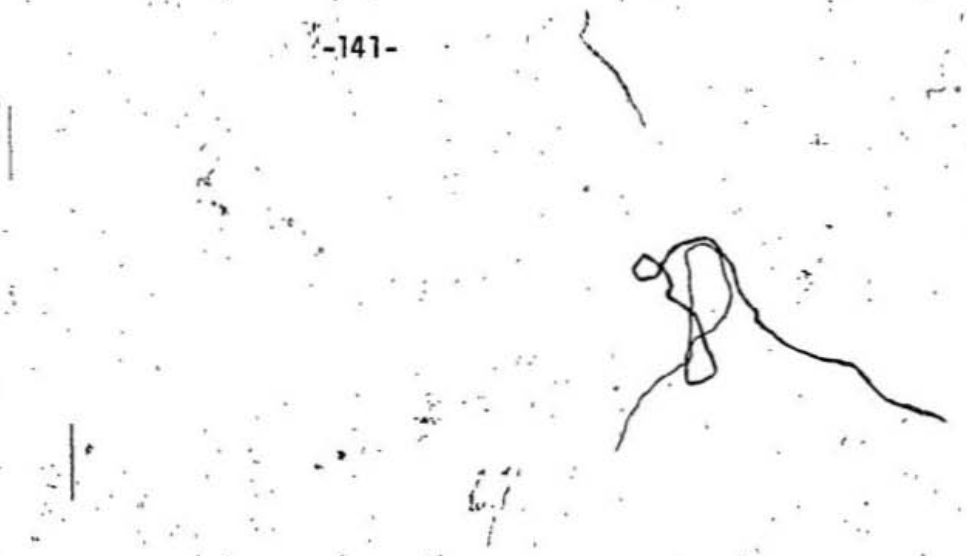
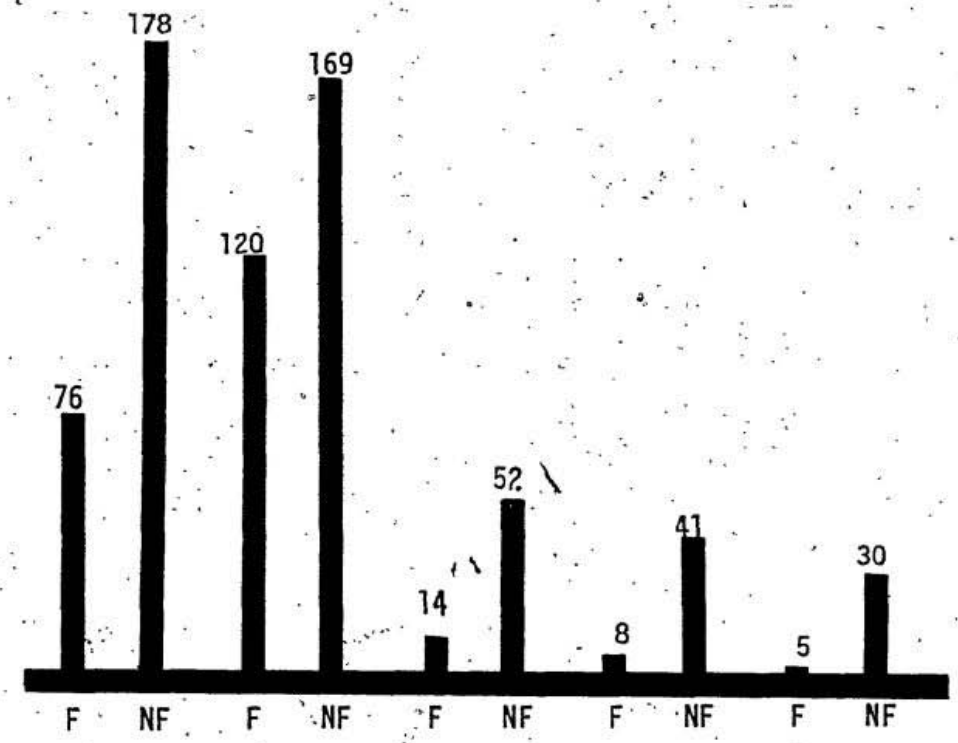


Figure 32. Relative numbers of feeding and non-feeding individuals and percentage of the population feeding of Asterias vulgaris in the five predation areas studied in Logy Bay.

F - feeding

NF - non-feeding



Percentage of Population Feeding	29.9	41.5	21.2	16.3	14.3
Area	A	B	C	D	E

E-II.3 (iib) Prey Selectivity (Table 23)

A.vulgaris showed a marked preference for M.edulis over any other prey. In areas of high abundance of mussels, A.vulgaris fed almost exclusively on them (in P.A.'s A and B, mussels represented 98.7 and 91.7% of their diet). Even in areas of sparse abundance of M.edulis, such as P.A.'s C and D, which are populated by the occasional mussel dislodged from the mussel beds during storms, etc., A.vulgaris selectively on these mussels rather than on more abundant prey items.

Of the secondarily preferred prey, echinoderms ranked highest. Of the total of the remaining 11 feeding observations S.droebachiensis represented the highest proportion (77.11) whereas Ophiopholis aculeata (3.11) and A.vulgaris (1.11) are occasional prey.

Molluscs, other than M.edulis, were preyed upon to a slightly lesser degree than echinoderms (nine observations). In terms of number of species, no clear preference for either bivalve or gastropod prey was noted. Of the two species of bivalve prey, however, H.arctica was preyed upon to the greater extent (four observations) with only one observation being made of predation upon Anomia sp. Two species of gastropods, Acmaea testudinalis and Margaretes costalis, were fed on to a limited degree. Only one feeding observation was noted for each of these species.

As previously noted for L.polaris, A. vulgaris was observed feeding on dead caplin on one occasion.

Six observations were made of A.vulgaris where the prey could not be determined. In these cases, the stomach was everted onto the rock substrate. Often fragments of Lithothamnion spp. were found

Table 23. Summary of the detailed feeding study of Asterias vulgaris listing prey species and the percentage each prey species represented of the total prey for each predation area.

Figures in brackets are the numbers of observations of feeding on the prey species.

Prey Species	Predation Area A	B	C	D	E	Total
Mytilus edulis	98.7 (75)	91.7 (110)	28.6 (4)	37.5 (3)	-	87.0 (207)
Strongylocentrotus droebachiensis	-	3.3 (4)	7.1 (1)	12.5 (1)	20.0 (1)	2.9 (7)
unknown	1.3 (1)	0.8 (1)	21.4 (3)	12.5 (1)	-	2.5 (6)
Hiatella arctica	-	0.8 (1)	7.1 (1)	25.0 (2)	-	1.7 (4)
Mallotus villosus	-	2.5 (3)	-	-	20.0 (1)	1.7 (4)
Ophiopholis aculeata	-	-	21.4 (3)	-	-	1.3 (3)
Tonicella marmorea	-	-	-	12.5 (1)	20.0 (1)	0.8 (2)
Margaretes costalis	-	-	7.1 (1)	-	-	0.4 (1)
Anomia aculeata	-	0.8 (1)	-	-	-	0.4 (1)
Acmaea testudinalis	-	-	-	-	20.0 (1)	0.4 (1)
Bryozoan	-	-	-	-	20.0 (1)	0.4 (1)
Asterias vulgaris	-	-	7.1 (1)	-	-	0.4 (1)

in the folds of the cardiac stomach. Whether individuals were feeding on the actual plant material or on the fauna associated with the Lithothamnion could not be determined.

E-II.3 (iii) Crossaster papposus

E-II.3 (iiia) Percentage of Population Feeding (Fig. 33)

A large percentage of all observed C.papposus was feeding during the predation study. Predation Area D had the greatest percentage of individuals feeding (60%) followed closely by P.A. E (50%). Of the ten individuals examined in P.A. C, only two or 20% were observed to be feeding.

E-II.3 (iiib) Prey Selectivity (Table 24)

C.papposus demonstrated a wide prey diversity ranging from coelenterates and echinoderms to the occasional meal of molluscs. The species most frequently preyed upon was Metridium senile, representing 100%, 41.7% and 30% of its diet in areas C, D, and E, respectively. Echinoderms (including S.droebachiensis, L.polaris, A.vulgaris and Psolus fabricii) were also found to constitute a major part of its diet, but no species could be considered individually important.

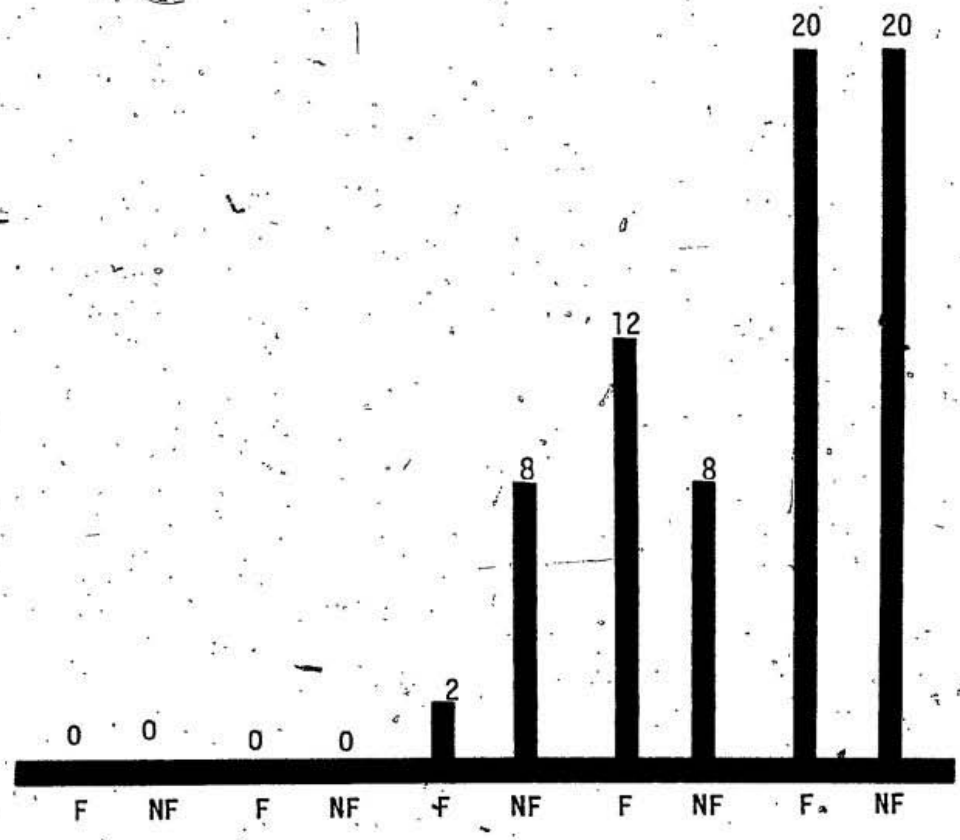
Two observations were recorded of C.papposus feeding on chitons.

Several observations were recorded of C.papposus apparently feeding on hydroids or bryozoans, and six observations were made of C.papposus with its stomach extended in the typical feeding position, yet no definite prey could be identified. In these cases, traces of algae (e.g. Ptilota seratta) were found on the rock substratum under the everted stomach. Since no cases of C.papposus feeding upon algae

Figure 33. Relative numbers of feeding and non-feeding individuals and percentage of the population feeding of Crossaster papposus in the five predation areas studied in Logy Bay.

F - feeding

NF - non-feeding



Area	A	B	C	D	E
Percentage of Population Feeding	0	0	20.0	60.0	50.0

Table 24. Summary of the detailed feeding study of Crossaster papposus listing prey species and the percentage each prey species represented of the total prey for each predation area.

Figures in brackets are the numbers of observations of feeding on the prey species.

Prey Species	Predation Area					Total
	A	B	C	D	E	
Metridium senile	-	-	100.0 (2)	41.7 (5)	30.0 (6)	38.2 (13)
unknown	-	-	-	16.7 (2)	20.0 (4)	17.6 (6)
Strongylocentrotus droebachiensis	-	-	-	16.7(2)	10.0 (2)	11.8 (4)
Hydroidea	-	-	-	-	15.0 (3)	8.8 (3)
Leptasterias polaris	-	-	-	8.3 (1)	5.0 (1)	5.9 (2)
Tonicella marmorea	-	-	-	-	10.0 (2)	5.9 (2)
Ectoprocta	-	-	-	8.3 (1)	5.0 (1)	5.9 (2)
Asterias vulgaris	-	-	-	-	5.0 (1)	2.9 (1)
Psolus fabricii	-	-	-	8.3 (1)	-	2.9 (1)

have been reported in the literature, either "hydroid" or "bryozoan" was recorded when they were present or "unknown" was recorded when neither was present. The possibility of C.papposus feeding upon algae or material attached to the algae, for example, sea anemones, eggs; or having fed upon small animals which had already been digested, and could not be recognized, still remains.

E-II.3 (iv) Solaster endeca

E-II.3 (iva) General Field Observations

Few field observations were made of S.endeca feeding, since only four individuals were observed over the entire length of the field study and in some instances repeated observations were noted. No calculation of percentage of the population feeding could be determined since ingestion is such a short segment of the alimentary process. (See laboratory feeding observations and the description which follows).

Ingestion of prey was observed on only four occasions. On two of these occasions, the prey was Psolus fabricii and on the other two, Gucumaria frondosa.

On the day preceding the ingestion of one of the specimens of C.frondosa (May 5, 1970), a large C.frondosa was observed on the sand bottom approximately six meters from a specimen of S.endeca. The specimen of C.frondosa was in poor condition; it appeared to be unusually bloated and apparently incapable of contraction of the body wall even after repeated probing. On May 6, specimen #1 of S.endeca had moved out onto the sand bottom and had begun ingesting the holothurian. By May 8, only a small portion of the C.frondosa was visible extending out of the mouth of the predator. The same asteroid was observed on

May 12 and May 20 resting on the rock bottom near the edge of the sand. On each occasion that slight pressure was exerted on its aboral surface, some remains of the sea cucumber were forced out of the mouth. As no further observations were made of the digestion of this sea cucumber, the total elapsed time of digestion could not be calculated. Observed digestion, however, did take in excess of fifteen days.

E-III Laboratory Study

E-III.1 Materials and Methods

Two laboratory predation experiments were run on each of two occasions. In one set of predation experiments, 250 ml volume displacement of each of three prey species was added to two A-frame tanks. The prey species used were: M.edulis, S.droebachiensis, and Volsella modiolis. In tank one, nine L.polaris of three size classes (3 in each class) were placed. Class sizes were 4.5, 7.0, and 9.5 cms. (± 0.25) in radius.

Similarly, nine A.vulgaris of the size classes, 3.5, 4.5 and 7.5 cms. radius, were placed in tank two. All collected specimens were obtained on a dive at Bay Bulls, and the experiments were set up upon immediate return to the M.S.R.L.

Observations and recordings were made every 24 hours for 14 days, of the temperature, nature and amount of prey consumed, location of each sea star in its tank, and the number of feeding sea stars. Shells or tests of consumed prey were removed from the tanks, counted, measured, and replaced with specimens of approximately the same size. The sizes

measured were the maximum length and width of each M.edulis or V.modiolis shell and the test diameter of each S.droebachiensis.

For a second series of predation experiments, three Solaster endeca were placed in tank one, and five C.papposus in tank two. Each tank was supplied with the following prey species in the numbers indicated:

Asterias vulgaris	5
Leptasterias polaris	5
Strongylocentrotus droebachiensis	5
Cucumaria frondosa	5
Psolus fabricii	5
Henricia eschrichti	5
Metridium senile	10
Gersemia sp.	10

All specimens were collected at a depth of 100 feet near the southernmost end of Logy Bay near Devil's Point.

Outlet drains were covered with finely meshed nettings so that no organisms would be washed from the tanks.

Every 24 hours for a period of 21 days, the numbers of each of the prey species were counted and recordings were made of any prey species that had been fed upon by either predator species, and of the water temperature in each tank. Any prey that had been eaten was replaced by a healthy specimen.

E-III.2 Food Preference Experiments

E-III.2 (i) Asterias vulgaris and Leptasterias polaris

Of the three prey species presented to these asteroids, only M.edulis was fed on to any extent. V.modiolis was not preyed upon by either species, and only one specimen of S.droebachiensis was eaten. (This specimen was eaten by A.vulgaris). Significant

differences existed between the rate of feeding for each species. For the duration of the experiment, A.vulgaris consumed 140 mussels, whereas L.polaris consumed only 35. The average number of M.edulis eaten per individual asteroid per day was 1.2 and 0.3 respectively. Values of number eaten per day were not constant over the duration of the experiment.

In the A.vulgaris tank, the number of M.edulis eaten increased steadily from a value of one to a value of 15 eaten per day between the first and the eighth day of the experiment. The feeding rate then remained relatively constant varying between 14 and 17 until the completion of the experiment. L.polaris also reached a peak in feeding rate on the eighth day; however, the feeding rate decreased rapidly afterwards until the eleventh day when no mussels were eaten. For the twelfth and thirteenth days, the feeding rate again peaked with six and five mussels being eaten respectively.

No clear correlation existed between number of M.edulis eaten per day and temperature. Although rate of consumption of mussels increased with a drop in temperature at day eight, no resultant decrease in feeding rate occurred between days 11 and 13 when the temperature again rose to the initial temperature. It is assumed, rather, that both species required a 'period of acclimation' to adjust to the new conditions of the laboratory, such as changes in light regime, temperature, dissolved oxygen concentration, and salinity. For A.vulgaris, this period appeared to last approximately seven days before feeding rate became constant. L.polaris never did achieve a constant rate of feeding.

Although this experiment was not designed to determine whether A.vulgaris or L.polaris fed selectively on a specific size class of M.edulis, some degree of size preference became evident. A.vulgaris did not feed on any specimen of a length greater than 41 mm. L.polaris also appeared to feed selectively on the smaller size classes because only one specimen of a length greater than 40 mm. was consumed (actual size was 62 mm. in length).

E-III.2 (ii) Crossaster papposus and Solaster endeca

Crossaster papposus

During the initial 21 days of experimental observations of this species, Henricia eschrichti was its major prey, representing five of the seven prey items consumed. Single specimens of A.vulgaris and L.polaris rounded off the 21 day diet of the experimental C.papposus.

At the end of an additional 14 day period in which no replacement of consumed animals was made, the following prey items were observed to have been fed upon: H.eschrichti (3), M.senile (2), and Gersemia sp. (2). Throughout the 35 days of experimentation which ran from July 15, 1971 to August 30, 1971, the water temperature fluctuated between 9.0 and 16.0°C.

Solaster endeca

The duration of this feeding experiment proved to be too short for any valid conclusion regarding prey selectivity to be reached. During the experiment, the following prey items were consumed: L.polaris (2), H.eschrichti (1), and P.fabricii (1).

E-III.3 Additional Feeding Observations of S.endeca

Ingestion, digestion, and egestion of a P.fabricii by S.endeca was examined for a period of twelve days. On January 20, 1971, a large specimen (about 20 cm. in radius) of S.endeca was observed in a humped position over an apparently healthy specimen of P.fabricii measuring approximately 15 cm. in length. For about three days, the predator remained mounted on the undamaged prey with its stomach and peristomial membrane enveloping the posterior dorsal surface of the sea cucumber. By the fourth day, however,the specimen of P.fabricii had lost a large percentage of its coelomic fluid and its ingestion was then rapidly completed.

The predator, which had remained in roughly the same location in the tank, moved then to a darkened area. By the eighth day (four days after ingestion), the first 'cleaned' Psolus plate appeared at the mouth of the starfish. Between the eighth and twelfth days the predator was very active, often tracing and retracing the same path as it moved around the tank. A large pile of Psolus plates was observed on the thirteenth day at a distance of approximately two meters from the predator suggesting that egestion took place on the twelfth day. Since no other plates were observed afterwards, the total alimentation period was assumed to be twelve days.

E-IV Summary of Feeding Observations

In addition to observations made during the preliminary and detailed field feeding studies and laboratory food preference experiments, many casual feeding observations were made in the laboratory and in the

Table 25. List of prey of Leptasterias polaris from field and laboratory observations.

Phylum	Class	Species	Location of Observation
Mollusca	Bivalvia	Mytilus edulis	Logy Bay
		Hiatella arctica	Logy Bay
		Musculus discors	Logy Bay
		Anomia sp.	Logy Bay
		Placopecten magellanicus (Gmelin)	Laboratory
		Mya arenaria L.	Laboratory
		Volsella modiolis	Logy Bay
	Gastropoda	Thais lapillus	Logy Bay
		Buccinum undatum	Logy Bay
		Acmaea testudinalis	Logy Bay
		Margaretes costalis	Logy Bay
		Lacuna vincta	Logy Bay
		Littorina littorea L.	Laboratory
	Amphineura	Tonicella marmorea	Logy Bay
Arthropoda	Crustacea	Balanus balanoides (L.)	Laboratory
		Balanus balanus (L.)	Logy Bay
		Hyas araneus	Logy Bay
Echinodermata	Echinoidea	Strongylocentrotus droebachiensis	Logy Bay
Chordata	Pisces	Mallotus villosus	Logy Bay

Table 26. List of prey of Asterias vulgaris from field and laboratory observations.

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1 The specimen had been opened by a large specimen of Leptasterias polaris.

Phylum	Class	Species	Location of Observation
Mollusca	Bivalvia	*Mytilus edulis*	Logy Bay
		Hiatella arctica	Logy Bay
		Anomia sp.	Logy Bay
		Chlamys islandicus	Laboratory
		Placopecten magellanicus[1]	Laboratory
		Mya arenaria	Laboratory
		Volsella modiolis	Laboratory
	Gastropoda	*Thais lapillus*	Logy Bay
		Buccinum undatum	Laboratory
		Acmaea testudinalis	Logy Bay
		Margaretes costalis	Logy Bay
		Lacuna vincta	Laboratory
		Littorina littorea	Laboratory
	Amphineura	*Tonicella marmorea*	Logy Bay
Arthropoda	Crustacea	*Hyas araneus*	Logy Bay
Echinodermata	Echinoidea	*Strongylocentrotus droebachiensis*	Logy Bay
		Ophiopholis aculeata	Logy Bay
	Asteroidea	*Asterias vulgaris*	Logy Bay
	Holothuroidea	*Cucumaria frondosa*	Laboratory
Entoprocta	---	unidentified species	Logy Bay
Chordata	Pisces	*Mallotus villosus*	Logy Bay

Table 27. List of prey of Crossaster papposus from field and laboratory observations.

Phylum	Class	Species	Location of Observation
Echinodermata	Asteroidea	Asterias vulgaris	Logy Bay
		Leptasterias polaris	Logy Bay
		Henricia eschrichti	Laboratory
	Echinoidea	Strongylocentrotus droebachiensis	Logy Bay
	Holothuroidea	Psolus fabricii	Logy Bay
Cnidaria	Anthozoa	Metridium senile	Logy Bay
	Hydrozoa	Gersemia sp.	Logy Bay
		several unidentified species	Logy Bay
Entoprocta	---	several unidentified species	Logy Bay
Mollusca	Amphineura	Tonicella marmorea	Logy Bay

Table 28. List of prey of Solaster endeca from field and laboratory observations.

Phylum	Class	Species	Location of Observation
Echinodermata	Asteroidea	Henricia eschrichti	Laboratory
		Leptasterias polaris	Laboratory
		Asterias vulgaris	Laboratory
	Holothuroidea	Psolus fabricii	Logy Bay
		Cucumaria frondosa	Logy Bay

field. The prey of each species observed by means of these casual observations and the detailed studies, are included in tables 25, 26, 27, 28.

E-V Feeding by the Genus Henricia

E-V.1 Field & Laboratory Observations

In the study area, specimens of H.eschrichti were observed positioned on two types of fauna, a yellow encrusting sponge, Halichondria panicea, and a white encrusting colonial tunicate, Didemnum albidum (fig. 34). Often large concentrations of five or six were noted on sponge or tunicate surfaces measuring less than 0.25 meters square. Preference for either H.panicea or D.albidum as a a substratum could not be determined since H.panicea was observed in shallower water (5 - 15 meters approximately), and D.albidum was found in deeper water (15-30 meters approximately). No area was found with close proximity of both species. Specimens of H.eschrichti were rarely observed with stomach extruded and the majority were observed positioned on the sponge or tunicate either with all five arms flat against the substrate or with one or two arms slightly raised in the filter feeding position described by Rasmussen (1965). No evidence of damage was noted on the D.albidum, whereas small pocks were noted on the surface of H.panicea where the oral region of H.eschrichti was resting on the sponge.

In order to examine the Henricia-sponge relationship in more detail, a piece of living sponge (H.panicea) was placed in a wet table containing a number of H.eschrichti and Henricia sp. After a period of approximately one hour, three H.eschrichti and two H. sp. had mounted the sponge. Two repetitions were made of this experiment on the same

Figure 34. Colour photograph of Henricia eschrichti positioned on the encrusting tunicate Didemnum albidum.

day by moving the sponge to different locations, and in each case, Henricia gathered on the sponge. Attempts, however, on the following day to attract Henricia to the sponge were futile. A close inspection of the surface of the sponge revealed several large pockets where tissue had obviously been removed. The sponge in general appeared to be in poor condition, presumably a result of the method of collection and handling rather than a result of damage inflicted by Henricia.

To test the existence of macrophagy as an occasional method of feeding, a large collection of H.eschrichti (& Henricia sp.) were offered cut-up pieces of herring (Clupea harengus harengus (L.)). Within a day, many of the specimens (both species) affixed themselves to the surface of the flesh and had their button-like stomachs extruded. This experiment was repeated with pieces of scallop flesh with the identical result.

E-V.2 Discussion

The feeding mechanism in the genus Henricia was first commented on by Anderson (1960). Basing his hypothesis on histological observations of the digestive system of H.leviuscula (Stimpson) and H.sanguinolenta (O.F. Muller), he concluded that Henricia was not primarily a carnivore but rather a flagellary-mucous feeder relying on a well developed suspension feeding mechanism to provide the necessary nutrients. He tested his hypothesis by placing two starved specimens of Henricia in a fingerbowl containing Nile Blue Sulphate and a suspension of Mytilus sperm in sea water. He noted a stream of particles moving towards the mouth, most noticeably along the ambulacral grooves. Dissection of the specimens revealed "concentrations of dye particles" in the Tiedemann's pouches, specialized pumping structures found in members of this genus.

Shortly after Anderson's paper, Vasserot (1962) reported H.sanguinolenta as a predator of sponges. Rasmussen (1965) refuted Vasserot's hypothesis by carrying out feeding experiments that showed Henricia capable of filtering from suspension, diatoms and flagellates at the rate of 19.5% per hour. He further concluded that Henricia has a tendency to live in an "energy commensalism" with sponges and that damage to sponges was probably caused by digestive enzymes found in the mucous secretion, i.e. sponge damage was not the result of a conscious effort by Henricia to digest the sponge tissue, but a consequence of the filter feeding mechanism.

Observations of the feeding behaviour of H.eschrichti tend to support the hypotheses of Anderson and Rasmussen. H.eschrichti appears to demonstrate an "energy commensalism" not only with a species of sponge, but also with a species of tunicate. Since H.eschrichti positions itself on two distantly-related types of animal which are similar principally because of their current producing nature, it appears obvious that Rasmussen's hypothesis concerning the Henricia-sponge relationship is correct. Also, since no damage was evident on the heavily spiculated tunicin surface of D.albidum, H.eschrichti cannot be considered a predator of that species, and damage likely results on sponges merely because of their less resistant surface.

As evidenced by observation of feeding by H.eschrichti (and Henricia sp.) on dead herring and scallop flesh, members of the genus Henricia apparently do occasionally practise macrophagy. Macrophagy could only be induced in H.eschrichti (& Henricia sp.) on dead prey. No observations of active prey capture and feeding on living animals

were noted. Hence one would expect that the incidence of macrophagy is very low in the environment unless large quantities of dead animal tissue are present.

E-VI Summary of Asteroid Food Niches

E-VI.1 General

All six species of sea stars can be catagorized into three separate general food niches according to their food preferences:

(a) Mollusc-Echinoderm (A.vulgaris and L.polaris)

(b) Coelenterate-Echinoderm (S.endeca and C.papposus)

(c) Suspended particulate matter (H.eschrichti and Henricia sp.)

E-VI.2 Mollusc-Echinoderm Food Niche

Primarily A.vulgaris and L.polaris are predators of molluscs, but some evidence of feeding on sea urchins and brittle stars was noted. Although there appeared to be an almost complete overlap in the feeding niches of these two species, several differences were uncovered by means of field and laboratory observations. The following enumerated points summarize these differences.

1. In field studies, A.vulgaris demonstrated a greater preference for M.edulis than was shown by L.polaris both in areas of high (P.A.'s A & B) and low (P.A.'s C and D) prey abundance. Laboratory studies showed that the rate of feeding on this prey species was four times higher than by L.polaris.
2. Brittle stars and sea urchins were fed upon by A.vulgaris to a greater extent than were fed upon by L.polaris. Laboratory observations confirmed that both species fed to some extent on these species when other prey items were absent.

3. Gastropods formed a greater part of the diet of L.polaris than of A.vulgaris. Of the total number of observed feeding L.polaris in the field, 10.1% were feeding on gastropods (6 species), whereas the figure for A.vulgaris was only 0.8% (two species).
4. In general, a greater number of species of molluscs were observed being preyed upon by L.polaris than A.vulgaris (9 and 4 species, respectively).
5. The species varied in percentage of the population feeding in each predation area. A.vulgaris demonstrated a significantly higher feeding percentage in P.A's B, C, and E., whereas approximately equal values were observed for P.A.'s A and D. Predation areas B, C, and E had the common characteristic of having a steep slope.[1] This relationship appears to suggest that A.vulgaris has a greater capacity than L.polaris for feeding in areas of sloped bottom.

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[1] A slight discrepancy in the data appears evident here. While P.A.'s A, C, D and E had constant slopes between their boundaries, P.A. B had two slope components, a gently sloped part near the TL and a steeper sloped part on the landward side. Unfortunately all feeding data were grouped together for these two segments of P.A. B during field recordings. Two additional pieces of information are necessary to bring out here. The total percentage of feeding for this area is a result of both sloped areas, but the highest percentage of feeding took place on the steep slope, an area of high abundance of M.edulis.

E-VI.3 Coelenterate - Echinoderm (Asteroids and Holothurians) Food Niche

Laboratory and field feeding studies clearly demonstrated that both C.papposus and S.endeca fed on asteroids and sea cucumbers, but that only C.papposus was observed feeding on coelenterates. Many authors (Grieg, 1913; Blevgvad, 1914; Bull, 1934) list C.papposus and S.endeca as preying on similar prey items. Overlapping of the food niche did not appear as consistent as the A.vulgaris - L.polaris overlap. The following summary enumerates perceived differences between these species.

1. C.papposus was a much more voracious active predator of sea stars than was S.endeca. No field observations of S.endeca predation on asteroids was noted, indicating perhaps a low capacity for capture of sea stars by S.endeca.
2. Sea cucumbers appeared to be the primarily preferred prey of S.endeca as evidenced by their efficiency of capture of sea cucumbers and low incidence of feeding on other prey.
3. Sessile prey, such as M.senile, Gersemia sp., bryozoans, and hydroids also formed an important part of the diet of C.papposus, whereas S.endeca was never observed feeding on this type of prey.
4. Feeding rates of C.papposus appeared to be much higher than S.endeca based on laboratory observations.
5. Competition for similar food resources has tended to lead to different prey selectivity of the two species. S.endeca has specialized in sea cucumber prey and C.papposus has specialized in asteroid and coelenterate prey. A trend by C.papposus towards

selectivity of M.senile was indicated by field studies. However, laboratory studies indicated a preference for asteroid prey.

E-VI.4 Suspended Particulate Matter Niche

The food niches of H.eschrichti and Henricia sp. could not be separated on the basis of field or laboratory observations. Following the evidence presented by Rasmussen (1965) and Anderson (1960), these two species must be considered to be primarily suspension feeders. Some degree of macrophagy does occur on dead animal tissue (with the exception of dead sponge), but the two asteroid species could not be separated in this regard.

E-VII Discussion of Food Generalism and Prey Selectivity with Respect to Asteroid Distribution

E-VII.1 General

Field and laboratory studies showed that all four predatory species of sea stars individually fed on a variety of prey species with no one species constituting the sole source of nourishment. Menge (1972) in describing his work on L.hexactis, called this condition 'food generalism', a term originally discussed by MacArthur and Pianka (1966). Apart from being food generalists, all four predators demonstrated a marked preference or selectivity in their choice of prey. Both the aspects of generalism and selectivity must be examined very closely in order to establish the effect of prey distribution on the distribution of predators.

E-VII.2 Relationship of Prey Distribution to Asteroid Distribution

It is a well known fact that a predator must successfully feed on its prey often enough to provide the necessary energy input to

fulfill its energy requirements for life. Asteroids, being relatively slow moving, slow feeding, sedentary animals, must live in areas where there is available prey. Principally this means that sea stars are incapable of feeding in one location and moving off to another distant area to carry out other activities. The effect of this hypothesis is that sea stars must be found in areas where there is a suitable abundance of prey.[1]

Since all four predatory species found in the study area proved to be food generalists, their distributions are not dependent upon the distribution of one or more species. The only restriction is that at least one prey species must be of adequate abundance and availability to supply the energy requirements of the predator. Food selectivity, however, functionally operates in the opposite direction. Instead of dispersing distribution, food selectivity would tend to concentrate predators in the area of greatest abundance of their preferred prey.

Let us consider the food niches of the various sea stars and examine the effect of the opposing principles of generalism and selectivity.

A. The Mollusc-Echinoderm Food Niche

Both A.vulgaris and L.polaris demonstrated a high degree of food generalism. In the study area we have seen that both species repeatedly fed on at least ten prey species. Since representatives of these prey species were found in all areas of the study area, these

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[1] Implicit in the very nature of generalizations such as this one is the concept of an exception. A suitable exception which might be forwarded is that sea stars can live for extended periods of time in the absence of prey by reabsorbing stored energy reserves.

asteroid species were not absolutely excluded from any one area. Evidence that each species was selective in feeding on M.edulis was overwhelming. Hence prey selectivity had the effect of concentrating the abundance of A.vulgaris and L.polaris in areas of highest abundance of their primarily preferred prey, M.edulis.[1] Also evident from feeding studies was that A.vulgaris demonstrated a greater preference for this bivalve than did L.polaris. The comparative effect was that A.vulgaris was more abundant in the MAL zone, an area of extreme abundance of M.edulis and L.polaris was more abundant in the cliff area, an area where M.edulis was more sparsely distributed.

B. Echinoderm - Coelenterate Niche

The principles of food generalism and selectivity cannot be applied to the two asteroid predators prosecuting this feeding niche in the same manner as they were applied to the distribution patterns of A.vulgaris and L.polaris. Although suitable prey was available in all parts of the study area, C.papposus and S.endeca were restricted to P.A.'s D and E (C.papposus were also observed in the lower portion of P.A. C, i.e. TLQ's 11 and 12). This restricted distribution pattern directly negates the relationship between predator distribution and the food foraging strategy previously associated with food generalism; hence, some other causal relationship must be operating.

Distribution patterns of both species also contradict the hypothesis that prey selectivity would tend to concentrate predators

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[1] Although this hypothesis is proposed without consideration of other possible factors affecting their distribution, it cannot be overstressed that a multifactorial causation is emphasized throughout this thesis.

in the area of greatest abundance of their prey. The detailed field feeding study demonstrated that C.papposus had a preference for the sea anemone, M.senile. However, the area of greatest abundance of sea anemones is P.A. C (between TLQ's 6 & 10), an area poorly populated by C.papposus. Similarly, if asteroids are considered to be their preferred prey (laboratory studies), one would expect C.papposus abundance to be skewed towards shallow water where the absolute abundance of asteroid species is highest. The picture becomes somewhat clearer, however, if we consider the distribution patterns of H.eschrichti and C.papposus. In laboratory food preference experiments, H.eschrichti was shown to be preferred by C.papposus over both sea anemones and other asteroid species. As we have seen in section C-II.2(iii), the distribution of H.eschrichti was greatest in sloped deep water bottoms, a depth range where C.papposus was abundant. However, the peak abundance of C.papposus did not correspond with the peak abundances of H.eschrichti in areas of steep slope.

Similarly the distribution pattern of S.endeca, rather than demonstrating a positive correlation with preferred prey abundance appeared to demonstrate a strong negative correlation.[1] In the study area, as previously mentioned, sea cucumber abundance was low, probably as a result of heavy predation pressure exerted by the combined efforts of S.endeca and C.papposus, whereas in areas of slightly shallower depth where neither predator was present, large numbers of holothurians were noted. This situation was especially true of Dyer's Gulch where

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[1] This relationship also existed for C.papposus since it was also shown to be a predator of sea cucumbers.

a large population of Psolus fabricii existed, and of the area extending landward from the study area where C.frondosa was abundant. Discontinuous abundances were also observed in areas of equal depth. While collecting S.endeca and C.frondosa for laboratory feeding and light preference studies in a deep water area near the southernmost edge of Logy Bay, the author noted that areas of high abundances of sea cucumbers and no S.endeca (or C.papposus) were alternated at the same depth with areas of high predator abundance and low holothurian abundances.

As a result of the application of food generalism and food selectivity to predator distribution, we find ourselves with the following contradictory conclusions:

1. Food generalism allows A.vulgaris and L.polaris to inhabit any area in the study area, whereas, S.endeca and C.papposus have restricted distributions even though abundant prey exists in all areas of the study area.
2. Food selectivity has the apparent effect of causing concentrations of L.polaris and A.vulgaris in areas of high abundance of their primarily preferred prey, but results in low abundances of prey where S.endeca and C.papposus are present.

First let us deal with the food generalism contradiction. The restricted distribution pattern of C.papposus and S.endeca suggests that other factors besides prey distribution affect the distribution patterns of these predators. Since both predators apparently survive in areas of low preferred prey abundance, the strategy of food generalism

is most likely being employed. In other words, S.endeca and C.papposus are capable of reducing the abundance of their primarily preferred prey to such an extent that they must resort to feeding on other prey species to survive in an area. Since their distribution is restricted, they remain in a specific area rather than foraging in adjoining areas where prey abundance is greater. Their feeding strategy appears to be to wait for their primarily preferred prey to migrate into their feeding area rather than emigrating to other areas in search of prey. Being food generalists allows them the facility to employ this strategy of waiting.

Several reasons may be forwarded as to why C.papposus and S.endeca decimate the populations of their primarily preferred prey, whereas L.polaris and A.vulgaris do not. Mussels form large aggregations of closely packed individuals and are confined to a relatively narrow depth range. Secondary settlement of mussel larvae occurs primarily in areas populated by adult mussels, (Bayne, 1964); hence, mussel beds have a high rate of recruitment. Although predation pressure by asteroids may be high in mussels beds, the rate of recruitment is high enough to maintain the population density in a state of equilibrium.

Holothurians have a much larger depth range and recruitment is not dependent on the presence of adults. Since abundance of holothurians is very diffuse, S.endeca and C.papposus may quite easily decimate a population within a specific area.

One other factor may be important in these feeding strategies. Since sea cucumbers are motile, S.endeca and C.papposus can remain within a certain territory and wait for the immigration of sea cucumbers.

Mussels, on the other hand, are relatively immobile as adults. Hence, L.polaris and A.vulgaris would have to seek out their prey.

Considered in this way, then, food generalism can have the effect of diffusing a population of predators into areas not populated by their primarily preferred prey, or may allow predators to remain in a specified area even though their primarily preferred prey is absent or in low abundance.

Food selectivity can affect the distribution of asteroids by causing concentrations in areas of high abundance of a primarily preferred prey item, or can reduce the abundance of the primarily preferred prey in an area by selective feeding by predators.

F. Reproductive Biology

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F. Reproductive Biology

F-I Introduction

Several aspects of the reproductive biology of sea stars may be important in affecting the distribution of a species. Through the combined efforts of a number of researchers, most of these aspects have been described for these species of sea stars in other areas. What remained to be done for this study was to verify that sea stars in this area actually practised reproduction in the same manner as described for other areas, to establish the brooding and spawning temporal cycles of sea stars in the study area, and to consider these aspects in their relationship to the spatial and temporal distribution patterns of these species as discussed in sections C-II and C-III.

F-II Materials and Methods

Observations of aspects of the reproductive biology were made employing an opportunistic strategy. Whenever a sea star was observed spawning or brooding, dates, nature of eggs, characteristic activities, and any other observations directly related to distribution or reproduction were recorded. Specific studies of brooding L.polaris were carried out by recording the location of brooding individuals (observations being made during feeding studies), and by photographic analysis of the brooding activity of an individual L.polaris located on TLQ 4, from February 9 to July 14, 1971. Similar studies were attempted for H.eschrichti, but were unsuccessful because of difficulties in locating brooding individuals.

F-III Field & Laboratory Observations of Spawning and Brooding Activities

F-III.1 Asterias vulgaris

One individual (male) was observed spawning in Logy Bay, July 29, 1971. No evidence of endemic spawning was visible although three other individuals of the same species were observed within a meter of the spawning individual. A spawning period of July 14 to August 17 was established from observations of spawning A.vulgaris in the laboratory. Endemic spawning was of common occurrence in the laboratory.

F-III.2 Leptasterias polaris

F-III.2 (i) Spawning and Brooding Periods

The spawning period of this species was determined by the occurrence of incipient brooding females. Some yearly variability existed as to the commencement of the brooding period. In 1971, the first brooding individual was observed on February 2 in Logy Bay, whereas in 1972 and 1973, brooding individuals were first observed in mid January.

F-III.2 (ii) Brooding Behaviour

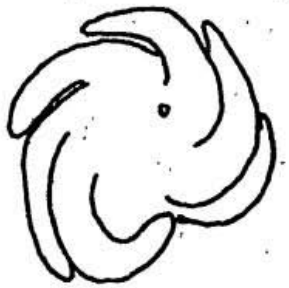
One brooding individual was photographed during the TLQ photographic series on TLQ 4. This specimen adopted the typical brooding position on February 9 (see fig. 35), and remained brooding the eggs until July 14. In the typical brooding position, each arm is bent sideways, touching the next so that the sea star lying flat on the substrate covering the eggs resembles a pinwheel. During the brooding period, the rotation of the arms alternated between clockwise and

Figure 35. Outline drawings of the brooding positions adopted by a specimen of Leptasterias polaris located in TLQ-4, from Jan. 12 to July 21, 1971.

JAN 12 JAN 26 FEB 2

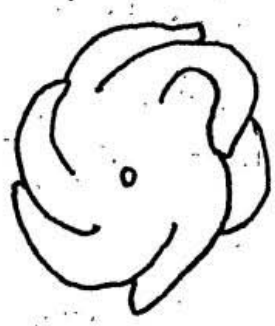
FEB 9 FEB 23 MAR 2

MARCH 9 APRIL 6 MAY 4

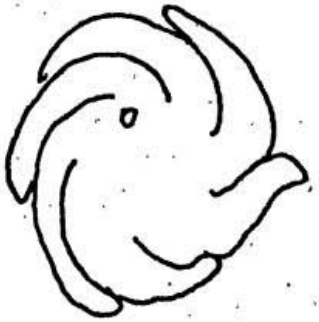


MAY 11

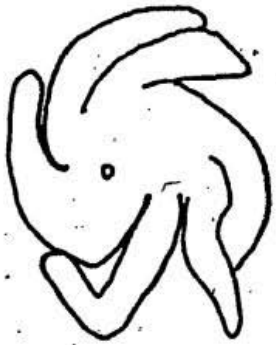
MAY 19



MAY 26



JUNE 9



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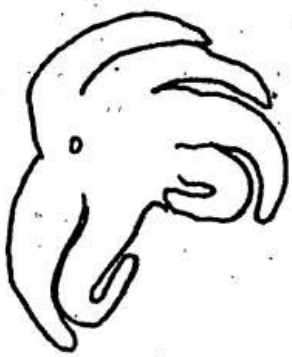
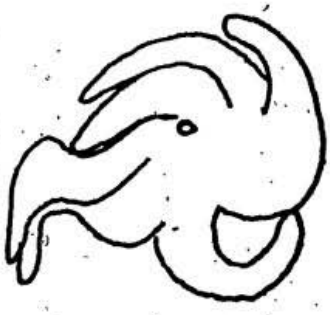
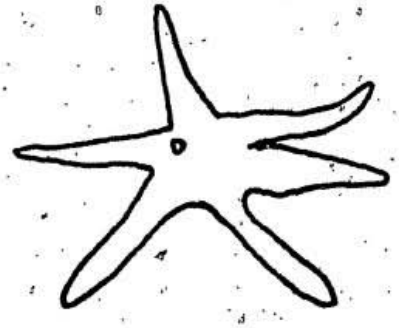


JULY 1

JULY 7



JULY 14



JULY 21

counterclockwise. From February 9 to June 17, no gaps were visible between each arm; however, from June 17 to July 14, gaps appeared between one or more arms. In general, eggs were laid flat on the rock substrate, forming a disc, two to three eggs in thickness with a diameter varying between 2/3 and 5/6 of the diameter of the brooding sea star.

F-III.2 (iii) Location of Brooding Activity

No extensive aggregations of brooding sea stars were evident in Logy Bay; however, some degree of location selection was noted. During the brooding period, the number of brooding individuals and number of non-brooding individuals was recorded for each of the predation areas (A-E).[1]

An examination of Table 29 which sumamrizes the results of this study, reveals a high percentage of individuals were brooding in P.A. C, and decreasing percentages occurred moving in either direction away from this area.

A situation worthy of note and comparison with Logy Bay occurred at Bay Bulls, where an extensive aggregation of brooding L.polaris was observed on February 4, 1971. Since this aggregation had been previously observed in October, 1970, it was not suspected to have been formed as a result of migration related to spawning behaviour, but as a result of high prey abundance. Also, owing to its

---

[1] These values are only important in determining the brooding to non-brooding ratios, and have no validity as relative abundance of L.polaris in each P.A. because the times spent in collecting data in each area differed.

Table 29. Numbers and percentages of brooding Leptasterias polaris per predation area.

Predation Area	No. Brooding Individuals	Total No. Individuals Observed	% Brooding Individuals per Area	% of Total Population Brooding per Area
A	1	66	1.49	1.43
B	13	171	7.07	18.57
C	17	95	15.12	24.29
D	8	82	8.89	11.43
E	1	78	1.27	1.43

location next to a cliff at right angles to the direction of swell, this area was more protected than the immediately surrounding area. On February 4, approximately 30-40% of the aggregation was brooding and on a return dive, April 15, 1971, it was estimated that the percentage brooding had increased to 40-50%.

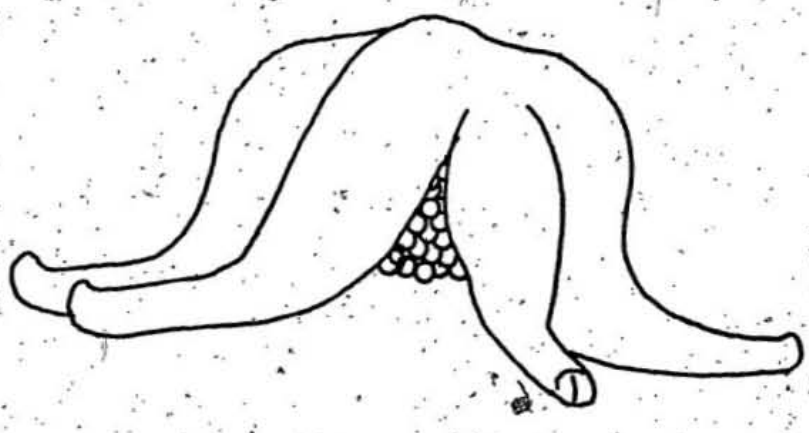
F-III.3 Henricia eschrichti

Only two individuals were actually observed brooding in Logy Bay, even though an extensive effort was undertaken to find evidence of this phenomenon. The dates of these observations were June 29, 1970, and May 25, 1971. In the laboratory, four spawning H.eschrichti were observed on February 1, 1971. In the brooding position (fig. 36), eggs are held in the oral region, arms are pulled together in a similar position, as described by Chia (1966) for L.hexactis, and attachment to the substrate is made by the distal 1/3 to 1/2 portion of each arm. The eggs of one of the spawning females were measured with a micrometer and found to be 1.16 mm. (average of 10 eggs), and the total number of eggs laid by this individual numbered 227. Although a minimum of ten individuals of this species was maintained in a wet bench from 1970 to 1973, spawning and subsequent brooding activity was only observed in 1971.

F-III.4 Crossaster papposus and Solaster endeca

No observations were made of spawning activity of these species in their natural environment in Logy Bay. Spawning by S.endeca was observed on two occasions in the laboratory, April 14, 1970, and April 11, 1973. On each occasion, between 500 and 1000 large, red, yolky eggs were laid. Observations of C.papposus (male) spawning

Figure 36. Drawing of the brooding position of Henricia eschrichti.



were restricted to one occasion, April 11, 1973, which appeared to be triggered by a number of other spawning species (S.endeca, H.eschrichti, Strongylocentrotus droebachiensis, and Ophiopholis aculeata).

F-IV Summary

In general, the aspects of the reproductive biology as demonstrated by the studied sea star species agreed with previously published descriptions. Table 30 summarizes the relevant reproduction characteristics of each species, indicating by an asterisk those aspects which were not verified by the present study (no contradictory observations were made; asterisks merely indicate observations not made). Credit is given to authors who were quoted in compiling the table. Since spawning and brooding periods are generally conceded to demonstrate large variations in different locations (Boolootian, 1966), the values presented in this table were obtained during the present study.

F-V Discussion

F-V.1 Factors Affecting Brooding Location of Leptasterias polaris.

A number of possible factors are now presented (Table 31) which may have an effect on the brooding percentage of the populations in each area. Each factor is analysed in terms of its possible effect on brooding percentages, and a possible hypothesis is proposed regarding the factors which are important in this relationship.

It is clear from this analysis, that no one factor is responsible

Table 30. Summary of the reproductive biology of the study area sea stars.

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[1] Galtsoff and Loosanoff, 1939.

[2] Gemmill, 1920.

* not verified by the present study.

Species	Spawning Period	Brooding Period	No. of Eggs	Egg Size	Larval Development	Larval Feeding Behaviour
Asterias vulgaris	mid July to mid August	none	many thousand[1]	small[1]	bipinnaria[1]	planktotrophic[1]
Leptasterias polaris	mid Jan. to mid Feb.	mid Jan. to mid July	200 - 500	1 - 2 mm	direct (no bipinnaria stage)	lecithotrophic
Henricia eschrichti	Feb.	Feb. to June (?)	200 - 300	1.2 mm	direct	lecithotrophic
Solaster endeca	April	none	few thousand[2]	1 mm	*larva	*lecithotrophic
Crossaster papposus	April	none	few thousand[2]	0.8 mm	*larva	*lecithotrophic

Table 31. Assessment of possible factors affecting the brooding locations of Leptasterias polaris.

FACTOR	POSSIBLE EFFECT	ANALYSIS	CONCLUSIONS
1. Temperature, conductivity, dissolved oxygen concentration.	To achieve a pattern such as the one described, an optimal range of T,C, and (O), would have to exist at area C.	For most of the year, no range of these parameters exists. Only during May to Sept. does a range exist.	Since brooding location selection would not take place during the period of stratification, temperature, conductivity, and dissolved oxygen concentration would not affect brooding location in the study area.
2. Slope	Certain inclination may enhance the probability of brooding success.	Areas C and E have most equal slope, yet do not have the same percentage of the population brooding.	Slope does not affect brooding location in the study area.
3. No. of brooding sites	If a limited number of ideally flat rock substrate brooding sites exist, sea stars may not be able to brood.	In each area, approximately equal numbers of possible brooding sites exist, yet all areas do not have an equal percentage of population brooding.	The number of brooding sites does not affect brooding location in the study area.
4. Pressure (depth)	If sea stars react to pressure, an optimal range may exist.	Since spatial distribution does not obey this relationship, brooding location should not be affected by this parameter.	Pressure does not affect brooding location in the study area.
5. Prey	Presence of nearby prey may cause starving females to leave eggs.	A higher prey abundance is found in area A than in C, and yet a greater percentage of the population was found to brood in area C than in A.	The presence of prey does not affect brooding location in the study area.
6. Density dependence	A higher proportion of brooding females may exist where abundance is high because of increased probability of fertilization of eggs.	Higher abundances of individuals occurred in areas A and B than in C, yet area C had the highest percentage of the population brooding.	Density does not affect brooding location in the study area.
7. Protection from water disturbance	Physical movement of water may cause sea stars to leave eggs.	Areas B and C are more protected than area A, and a higher percentage of the population was found to brood in these areas. Areas D and E are more protected than C, yet fewer brood in these areas.	Occurrence of water disturbance may explain why a greater number brood in area C than in B and A; however it cannot explain why E (a protected area) has a lower percentage of brooding individuals than area C.
8. Predators	Brooding females are very susceptible to predation. Predators may feed on brooding female or cause eggs to be abandoned.	Areas A and B are predator-free but C has predators and has a higher percentage of brooding than areas A and B. A higher number of predators exist in D and E than in C and low percentages of brooding were observed in D and E.	Occurrence of predators cannot be used to explain the gradient in numbers of brooding individuals from areas A to C, but may explain why brooding percentages are higher in C than in D and E.

for the differences in brooding percentages shown in the various areas. After individual consideration of each factor, three factors remain that apply to specific locations, and when considered together may explain this relationship. All three factors may operate if we assume that an equal proportion of females of the population in each area are capable of brooding eggs. It appears then that in shallow water (P.A.'s A and B), brooding activity is inhibited by water disturbance, and in deeper water (P.A.'s C and E) brooding activity is suppressed by predators of the brooding females. Density dependence also may account for the fact that P.A. D has a higher percentage of brooding because of its relatively low abundance of L.polaris predators, its protection from water disturbance, and its high L.polaris abundance.

The observations made at Bay Bulls tend to support this hypothesis for the following reasons:

1. A higher abundance of L.polaris existed in this area preceding the brooding cycle; hence, this brooding aggregation was in part due to yearly abundance in this area.
2. Even though the aggregation was restricted to shallow water, water disturbance was lessened by the proximity of a cliff preventing heavy exposure.
3. No natural predators, ie. C.papposus or S.endeca were found near the aggregation.
4. Factors one through five (Table 31) differed from P.A. C, and hence are considered relatively unimportant in determining the brooding percentage of a population.

F-V.2 Possible Effects of Reproductive Biology on Temporal and Spatial Distribution of Asteroids

In considering the effect of reproductive biology of an asteroid species on its distribution and abundance, three general relationships must be examined:

1. The effect of spawning on distribution.
2. The effect of brooding on distribution.
3. The effect of larval settlement on distribution.

1. The Effect of Spawning on Distribution

The possible effects of spawning on the distribution patterns of a species pose two questions: Does spawning cause any general migration of individuals to any particular location, and/or, does spawning have any apparent effect on the aggregative tendencies of a species? The former question can be assessed by examining the temporal distributions and determining whether any significant changes took place during the time directly preceeding and during the spawning periods. The latter question was assessed by general observations and inferences from temporal distribution of sea stars during spawning periods (ref: section C-II.3(ii)).

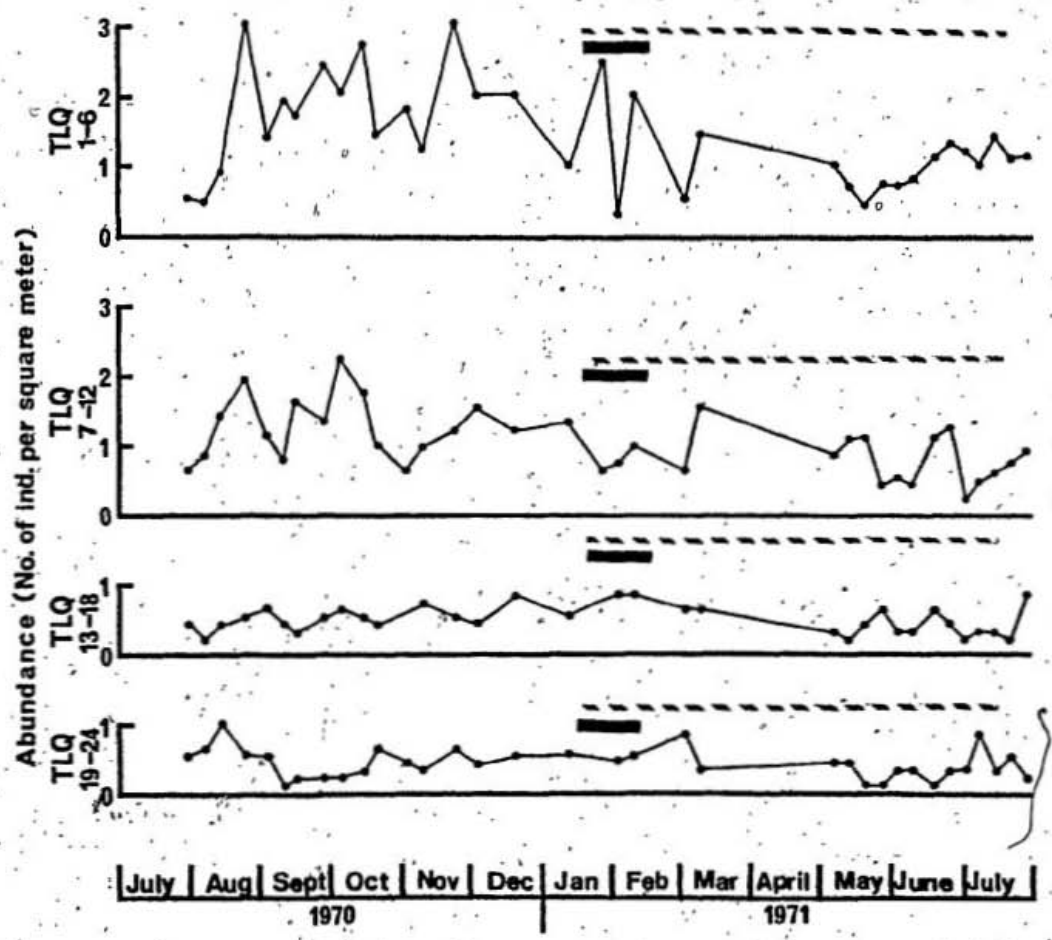
(A) Leptasterias polaris

In figure 37, the spawning period of L.polaris is indicated on a graph of temporal distribution in areas B (TLQ's 1-6), C (TLQ's 7-12), D (TLQ's 13-18), and E (TLQ's 19-24). No distinct migration associated with spawning can be clearly discerned in any of the regions; however, in area B, large fluctuations in abundance appear to indicate aggregative

Figure 37. Graph of temporal abundance of Leptasterias polaris with respect to four TLQ blocks, with brooding and spawning periods indicated.

spawning period.

brooding period


TLQ 1-6
TLQ 7-12
TLQ 13-18
TLQ 19-24
Abundance (No. of ind. per square meter)
0
1
2
3
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
April
May
June
July
1970
1971

tendencies within this area, but no large movements in and out of the area, ie. to deeper or shallower water. Compared with the rest of the year, no fluctuations of such amplitude take place. General observations do not, however, support this hypothesis for no large scale aggregative behaviour was noted in Logy Bay. The possibility of the occurrence of this phenomenon, however, is suggested from observations made of L.polaris in Bay Bulls, and from the possibility of actually not observing this phenomenon because of infrequent dives during this period.

(B) Asterias vulgaris

Again, no clear tendency of large scale migration was evident. In contrast to L.polaris, unusual fluctuation patterns did not characterize the time period before, during, or immediately after spawning (fig. 38). General observations (laboratory and field) indicated that spawning individuals were not associated with aggregations.

(C) Henricia eschrichti

Similarly, no extreme changes in abundance became evident during the spawning period (fig. 39).

Summary

In general, then, it appears that no changes in distribution patterns result from large scale migratory tendencies of the population associated with spawning. Aggregation formation associated with spawning may account for the extreme fluctuation patterns of L.polaris during the spawning period. Data for temporal distributions do not bear out the same aggregative tendencies for A.vulgaris and H.eschrichti.

Figure 38. Graph of temporal abundance of Asterias vulgaris with respect to four TLQ blocks, with spawning period indicated.

▬ spawning period

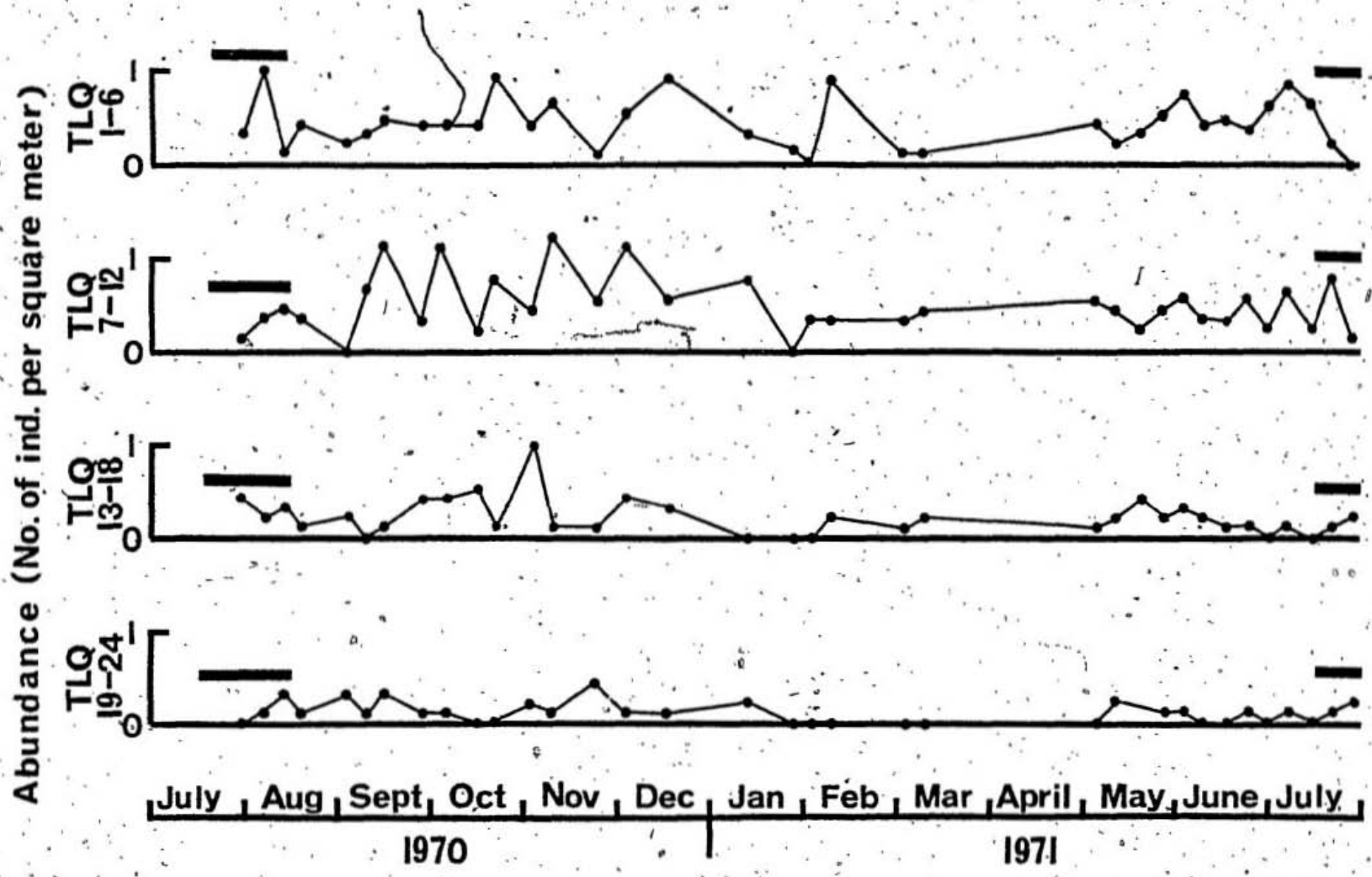
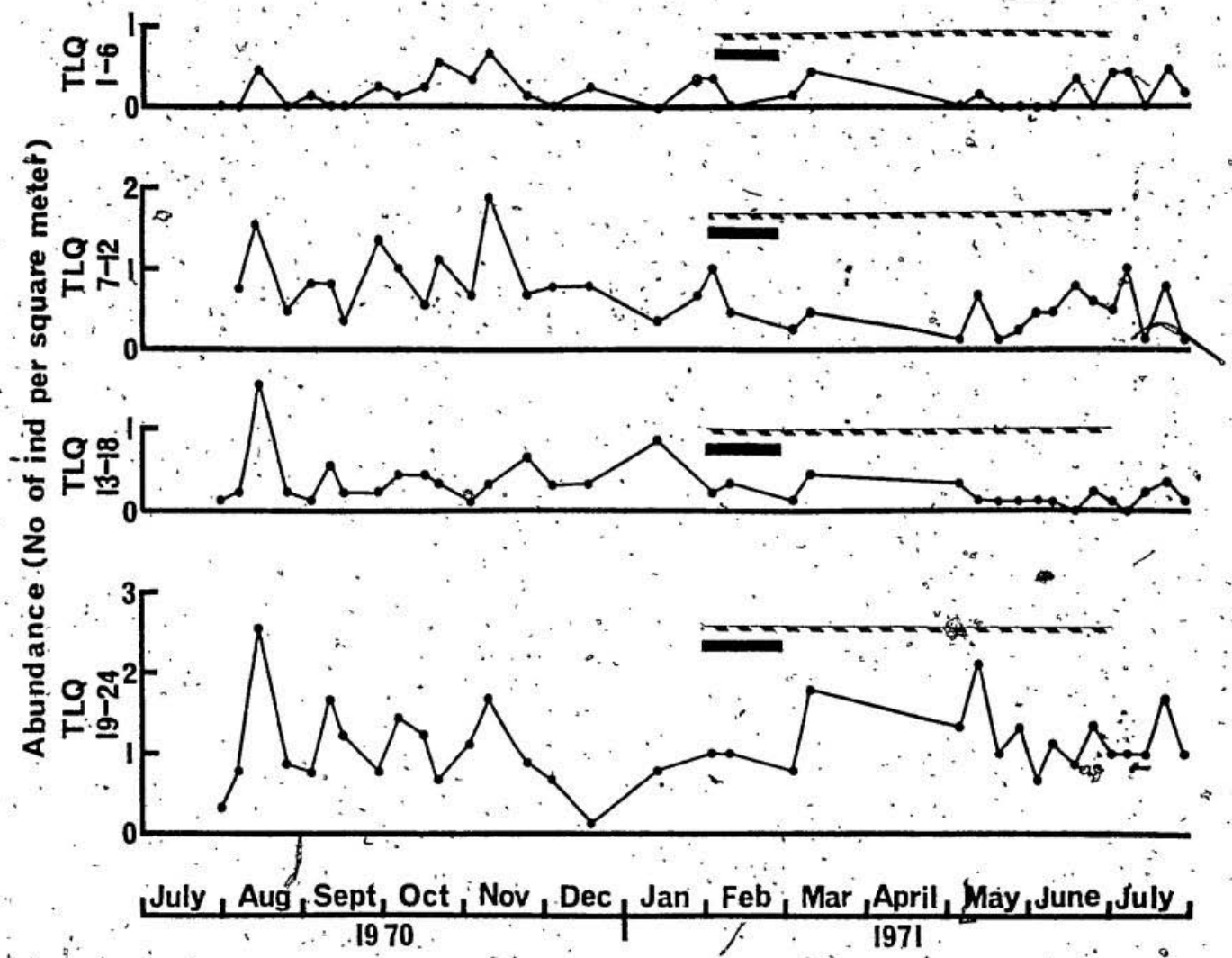

Abundance (No. of ind. per square meter)
TLQ 1–6
TLQ 7–12
TLQ 13–18
TLQ 19–24
0
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
April
May
June
July
1970
1971

Figure 39. Graph of temporal abundance of Henricia eschrichti with respect to four TLQ blocks, with brooding and spawning periods indicated.

spawning period

brooding period


TLQ 1–6
TLQ 7–12
TLQ 13–18
TLQ 19–24
Abundance (No of ind per square meter)
0
2
3
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
April
May
June
July
1970
1971

2. The Effect of Brooding on Distribution

If we assume that certain locations are more favourable for brooding than other areas, brooding behaviour has the effect on the adult population of concentrating more females in these areas. Since movement of L.polaris is limited, adults would tend to remain in the general vicinity of these areas from one brooding season to the next.

The second effect of selective brooding locations on distribution is that centres of abundance of juveniles occur in brooding areas. If no large scale movements of juveniles occur, the distribution patterns of juveniles would correspond to the distribution of brooding females. In this way, the distribution patterns of adults is perpetuated by the next generation assuming no migration and constant survival factors within the study area for successive generations.

3. The Effect of Larval Settlement on Distribution Patterns

Again, assuming no migration of individuals, and constant survival factors in all settlement areas, distribution patterns of a species would be dependent upon the distribution pattern of settling larvae. No direct evidence of this relationship is available for the study area, but strong supportive evidence is available from other sources. Analysis of settlement traps placed in Placentia Bay by the M.S.R.L. Mussel and Scallop Survey, indicated that the number of settled A.vulgaris larvae decreased with depth. This pattern coincides with the spatial distribution pattern obtained during this study of adult A.vulgaris abundance.

The second piece of evidence comes from the work of Galtsoff and

Loosanoff (1939, p. 110). Fig. 26 from their study has plotted the number of starfish set and number of adult starfish against depth. The distribution pattern of starfish set is almost identical to the distribution pattern of adults.

A similar argument can be used for C.papposus and S.endeca larval settlement. These species lay large yolky eggs, and larval feeding is lecithotrophic (Gemmill, 1920). Since these eggs and developing larvae are heavy (Thorson, 1950), and slightly negatively buoyant, settlement would tend to be in deeper water, coinciding with the adult population. In this way, a perpetual deep water distribution is maintained.

In general, then, we can conclude that settlement of larvae has the pronounced effect of perpetuating the distribution pattern of the adult.

G. Growth of Juvenile Asterias vulgaris

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G. Growth of Juvenile Asterias vulgaris

G-I Materials & Methods

A collection of sea stars was obtained from spat collectors which had been placed in mid-water in a protected area of Garden Cove, Placentia Bay on August 30, 1972, by researchers of the M.S.R.L. From seven collectors, retrieved on April 26, 1973, a total of 115 sea stars was removed, measured with calipers, and weighed on a Mettler balance.

G-II Results

All sea stars gathered by the spat collectors resulted from settlement of brachiolaria larvae and were all identified as A.vulgaris. Collectors also contained moderately abundant collections of M.edulis, Placopecten magellanicus, Anomia simplex (d'Orbigny), Anomia aculeata, and Hiatella arctica. Size (radius) and weight data were analysed by classing the data and determining the mean, standard deviation, and variance using the Wang desk computer programme for grouped data. Class intervals determined by the formula $\frac{\text{Range}}{\frac{\text{Range}}{\text{S.D.}} \times 4}$, were 0.03 gm., and 0.10 cm. for weight and radius, respectively.

A wide range of sizes and weights were recorded for the collected sea stars and are summarized as size-frequency, and weight-frequency in Tables 32 and 33.

Analysis of other spat collectors removed periodically from Placentia Bay determined that settlement of larvae took place during

Table 32. Size-frequency distribution of juvenile Asterias vulgaris collected by spat collectors in Placentia Bay.

Size Class (cm)	Class Mark (cm)	Frequency
0.21 - 0.30	0.25	3
0.31 - 0.40	0.35	9
0.41 - 0.50	0.45	9
0.51 - 0.60	0.55	13
0.61 - 0.70	0.65	12
0.71 - 0.80	0.75	11
0.81 - 0.90	0.85	24
0.91 - 1.00	0.95	15
1.01 - 1.10	1.05	9
1.11 - 1.20	1.15	7
1.21 - 1.30	1.25	2
1.31 - 1.40	1.35	0
1.41 - 1.50	1.45	1

Grouped Mean = 0.76; Variance = 0.06; S.D. = 0.25

Table 33. Weight-frequency distribution of juvenile Asterias vulgaris collected by spat collectors in Placentia Bay.

Weight Class (g)	Class Mark (g)	Frequency
0.0000 - 0.0300	0.0150	9
0.0301 - 0.0600	0.0450	14
0.0601 - 0.0900	0.0750	15
0.0901 - 0.1200	0.1050	12
0.1201 - 0.1500	0.1350	15
0.1501 - 0.1800	0.1650	12
0.1801 - 0.2100	0.1950	7
0.2101 - 0.2400	0.2250	6
0.2401 - 0.2700	0.2550	5
0.2701 - 0.3000	0.2850	2
0.3001 - 0.3300	0.3150	1
0.3301 - 0.3600	0.3450	6
0.3601 - 0.3900	0.3750	4
0.3901 - 0.4200	0.4050	4
0.4201 - 0.4500	0.4350	0
0.4501 - 0.4800	0.4650	0
0.4801 - 0.5100	0.4950	0
0.5101 - 0.5400	0.5250	2
0.5401 - 0.5700	0.5550	0
0.5701 - 0.6000	0.5850	1

Grouped Mean = 0.164

Variance = 0.0153

Standard Deviation = 0.123

the month of September. Therefore, the period of growth for these sea stars was October to April, or roughly seven months. The mean rate of growth per month, calculated using the mean values were 1.15 mm (radius increase) and 0.24 g (weight increase).

G-III Discussion

Growth has been shown by various researchers to vary according to size of individual (Galtsoff and Loosanoff, 1939), food supply (Mead, 1900; Galtsoff and Loosanoff, 1939), temperature (MacKenzie, 1969; Smith, 1940), competition (Menge, 1972), and other environmental parameters such as turbulence (Galtsoff and Loosanoff, 1939). Sea stars examined during this study were reared under a unique set of conditions and may have had a growth rate very dissimilar to sea stars found in the study area in Logy Bay. Logy Bay differs from the spat collector conditions by having a more turbulent environment, more competitors, more predators, and different food availability and abundance.

Previously published growth data for A. vulgaris and A. rubens (summarized in Table 34, from Halpern, 1970), list growth values (usually using radius R) much higher than those calculated for these sea stars.

Reasons for this discrepancy are probably due to the size of individual examined, the period of the year, and the physical parameters of the environment. The wide range of sizes and weights encountered in this study result most likely from the variable food supply found in the

Table 34. Summary of previous reports of the growth rate of *Asterias rubens* and *A. vulgaris*.

Species	Reference	Growth Per Month (mm)
Asterias rubens	Hancock, 1950	3.1
Asterias rubens	Bull, 1934	3.9
Asterias rubens	Orton and Fraser, 1930	4.1
Asterias rubens	Barnes and Powell, 1951	4.8
Asterias rubens	Vevers, 1949	5.0
Asterias vulgaris	Smith, 1940	10.2

spat collectors rather than variable periods of growth because of time of settlement. Settlement was observed to be over by the beginning of October; hence, all sea stars would have a very small range of growth period, ie. 7 months ± 1/2 month (maximum). Distribution of asteroid prey within the spat collectors was non-uniform; thus, the larger individuals may have had a greater food availability than the smaller individuals.

In summary, sea star growth rates as determined by this study are extremely low in comparison with growth rates of A.vulgaris and A.rubens determined at other locales, and may not be indicative of the growth rate of sea stars in the study area. Since growth rates may vary with the size of the individual and time of the year, these growth values cannot be considered representative of the overall growth rate of A.vulgaris found in Newfoundland waters.

H. Pull Capacity Experiments

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H. Pull Capacity Experiments

H-I Materials & Methods

A series of laboratory experiments was performed to determine whether sea star species varied in their capacity to remain attached to a specific substrate when pulled upon by an upward force directed along the oral-aboral axis.

H-I.1 Experimental Apparatus

Each sea star was placed in an area of a wet table bounded on either side by a board enclosure. The space between the boards formed a channel extending from the inflow pipe at one end to the outflow drain at the other end. The inflow pipe was positioned so that water was caused to flow parallel to both the surface of the tank and the enclosing boards. This apparatus was constructed to force the sea stars to attach to the substrate while withstanding a current directed along the channel.

A "Chatillon" temperature-compensated spring balance was hung above the tank by means of rope and pulleys to measure the maximum amount of pull each individual sea star could withstand. When tested, each sea star was fitted with a harness (fig. 40) which was attached to the hook of the spring balance by means of a metal ring.

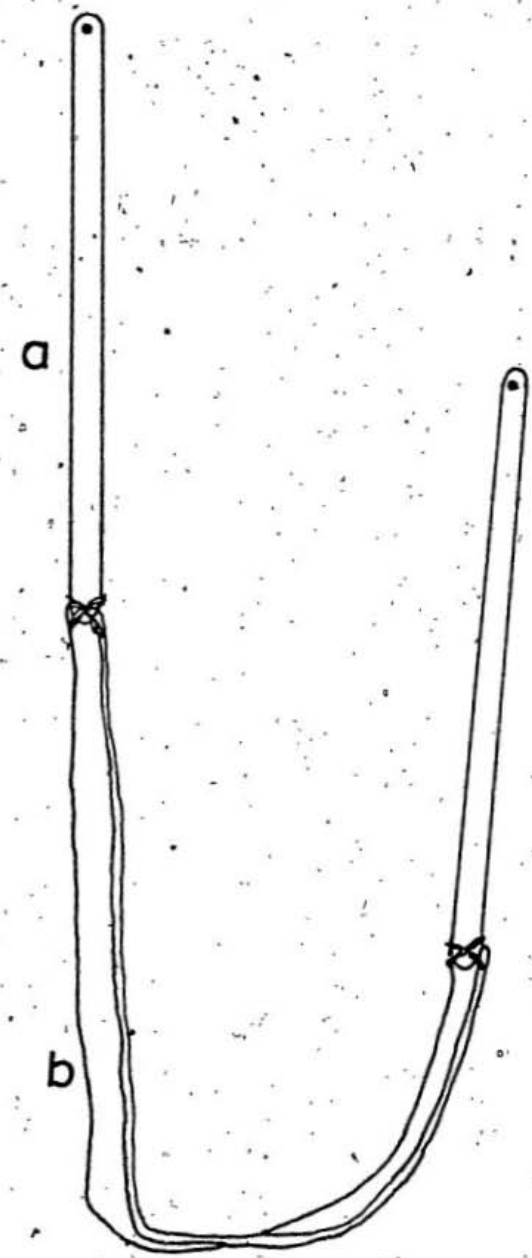
H-I.2 Experimental Procedure

Each tested sea star was placed in the channel and allowed to 'rest' momentarily. The water in the tank was then lowered by removing the drain pipe until only a small volume of sea water flowed past the sea star. At this point the drainage pipe was replaced and the inflow turned on, slowly increasing the current. This procedure of raising and lowering the water in the channel was repeated until all rays of

Figure 40. Drawing of harness used for Pull Capacity experiments. Actual size.

a - aluminum strip

b - chamois strip


a
b

the tested sea star were firmly attached to the substrate. Attachment was tested by pulling gently upwards on the sea star with the thumb and index finger, grasping the sea star on the lateral margins of each ray.

When successful attachment was achieved, the sea star was fitted with two harnesses. The metal ends of each harness were slipped onto the metal ring and the metal ring was hung on the hook of the spring balance (fig. 41). Position of the spring balance was then adjusted so that the pull exerted on the sea star would be perpendicular to the aboral surface directly above the centre of the central disc.

The free end of the pulley rope was slowly pulled by the investigator until a pull of four ounces was exerted on the sea star. After a 20-30 second period of adjustment, the force was again slowly increased, stopping at each ounce for approximately one second. The maximum pull that each sea star could withstand (ie. the poundage at which the sea star came free from the tank bottom) was recorded. Every sea star was tested in succession until three consecutive successful trials were completed. If any of the three trials could not be performed on an individual, that individual was replaced and not considered in the data. The number of individuals for each species that could not be tested was recorded. Ten individuals of L.polaris, A.vulgaris, and C.papposus were tested successfully, whereas only six S.endeca could be tested.[1] H.eschrichti could not be forced to attach

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[1] Only six S.endeca were tested because of a lack of experimental animals and not because of difficulty in testing them.

Figure 41. Drawing of the experimental apparatus used in studies of Pull Capacity of the several species of asteroids.

a - suspending bar

b - pulley

c - spring balance

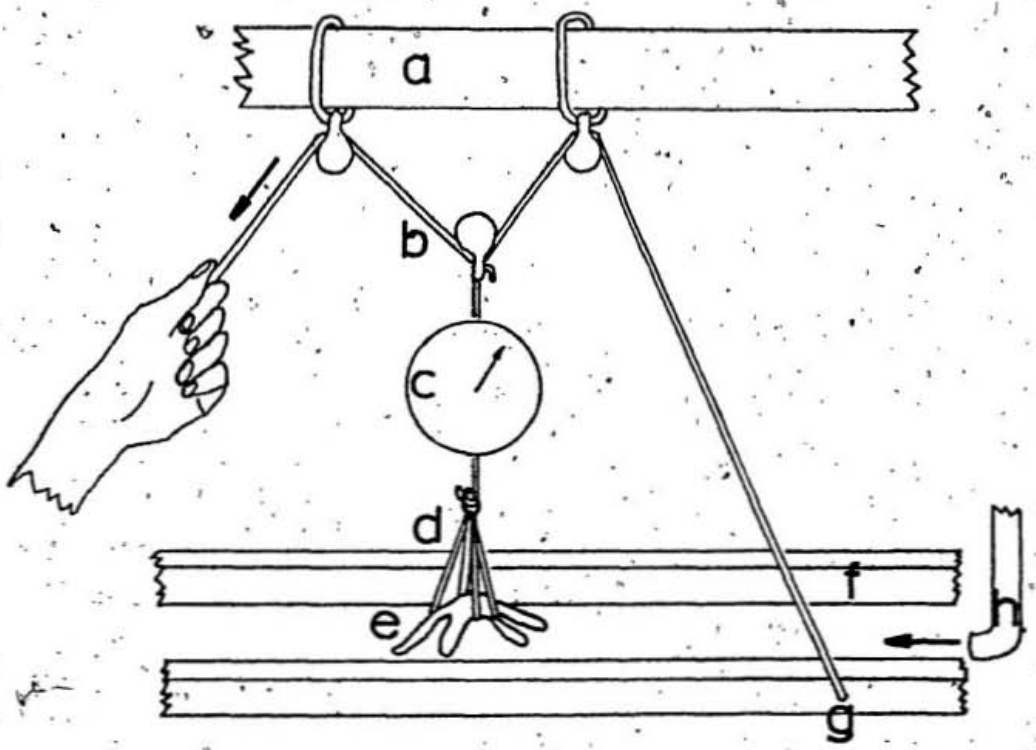
d - harness

e - sea star

f - board enclosure

g - fixed end of pulley rope

h - inflow pipe


a
b
c
d
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f
g
h

to the surface sufficiently well enough to withstand the minimum force (1 ounce). All values were converted to grams.

H-II Pull Capacity Results & Discussion

The data from these experiments were considered in three ways.

1. Pull Capacity (PC)

An absolute value expressing the maximum force a sea star can resist before it is pulled away from the substrate is presented only for comparison with previously published results. Since the tested values of pull capacity of a species may vary greatly with experimental method, substrate, size and physiological condition of individuals, and experimental conditions (primarily temperature), little stress is placed on these absolute values by this author.

Table 35 lists the experimental values obtained from the pull capacity experiments. The maximum value of 6010.2g obtained for L.polaris exceeds all published values for other species. The closest value hitherto published is 5500 g for Evasterias troscheli (Stimpson) measured by Christensen (1957). Other values, especially those for A.vulgaris (maximum 2438.1 g) fell well short of expectation. Christensen (unpublished, cited in Feder & Christensen, 1966), recorded a value of 4000 g for A.rubens, a closely related species. As previously suggested, these data are of little comparative significance because of variable experimental parameters. Means and standard deviations are listed in Table 42.

2. Pull Capacity/Radius (PC/R)

In order to compare values obtained from this experiment, PC was divided by R so that similarly sized individuals of each species

Table 35. Pull Capacity (g) of Leptasterias polaris, Asterias vulgaris, Crossaster papposus, and Solaster endeca for three trials.

	Leptasterias polaris			Asterias vulgaris			Crossaster papposus			Solaster endeca		
Trial No.	1	2	3	1	2	3	1	2	3	1	2	3
Ind. #1	3600.45	2466.45	3118.50	2268.00	737.10	765.45	141.75	28.35	28.35	935.55	538.65	226.80
2	1984.50	2806.65	1077.30	2097.90	737.10	992.25	453.60	311.85	595.35	283.55	113.40	28.35
3	5613.30	3912.30	3373.65	1332.45	1105.65	481.95	340.20	198.45	255.15	1304.10	878.85	737.10
4	5329.80	3515.40	1020.60	1077.30	113.40	28.35	141.75	28.35	28.35	992.50	652.05	935.55
5	4649.40	3912.30	2097.90	2438.10	708.75	481.95	1559.20	28.35	28.35	1162.35	731.10	632.70
6	4422.60	2041.20	992.25	632.70	113.40	113.40	113.40	226.80	425.25	1615.95	992.25	680.40
7	6010.20	2721.60	1757.70	481.95	396.70	198.45	56.70	85.05	113.40	-	-	-
8	4082.40	2636.55	907.20	481.95	425.25	311.85	85.05	113.40	255.15	-	-	-
9	2069.50	5670.00	1842.75	113.40	340.20	226.80	737.10	113.40	141.75	-	-	-
10	3458.70	2438.10	1814.40	963.90	1077.30	850.50	255.15	255.15	198.45	-	-	-

could be compared. Although an attempt was made to select approximately equal-sized individuals of each species for experimentation, a wide range of sizes resulted because of the small number of collected specimens from which selection was made. From these values, (PC/R) presented in Table 36, it can be seen that L.polaris had a value much higher than the other species, and that differences between the remaining species can be noted. To test the significance of these differences, two significance tests were applied to the data.

The first test, a two-way analysis of variance considered the PC/R values of the ten individuals (six for S.endeca) of each species for three trials to determine whether significant differences existed between individuals of a species, and whether significant differences existed between the first, second, and third trials. These data, presented in Table 37, showed that no significant differences did exist between individuals of L.polaris, A.vulgaris and C.papposus whereas significant difference did exist for S.endeca individuals. A significant difference between trials for species L.polaris, A.vulgaris and S.endeca but not for C.papposus is also shown by this table.[1]

In the second test, a one-way analysis of variance (Wang Programme) the significance of interspecific differences based on the first trial were examined. From these results listed in Table 38 we can see that the differences between the species, considered together,

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[1] These differences between trials are presented in the next section entitled: "Reattachibility".

Table 36. Pull Capacity / Radius (g/cm) of *Leptasterias polaris*, *Asterias vulgaris*, *Crossaster papposus*, and *Solaster endeca* for three trials.

	Leptasterias polaris			Asterias vulgaris			Crossaster papposus			Solaster endeca		
Trial No.	1	2	3	1	2	3	1	2	3	1	2	3
Ind. # 1	423.58	290.17	366.88	252.00	81.90	85.05	20.25	4.05	4.05	110.06	63.37	26.68
2	220.50	311.74	119.70	246.80	86.72	116.70	43.20	29.70	56.70	25.77	10.31	2.58
3	534.60	372.60	321.30	166.56	138.20	60.24	42.53	24.81	31.89	89.94	60.61	50.83
4	532.98	351.54	102.06	179.55	18.90	4.73	18.90	3.78	3.78	76.35	50.16	71.97
5	489.41	411.82	220.83	232.20	67.50	45.90	239.87	4.36	4.36	101.07	64.10	55.02
6	491.40	226.80	110.25	97.34	17.45	17.45	13.34	26.68	50.03	107.73	66.15	45.36
7	632.60	286.48	185.02	60.24	49.59	24.81	6.67	10.01	13.34	-	-	-
8	510.30	329.57	113.40	56.70	50.03	36.69	10.63	14.18	28.14	-	-	-
9	206.95	567.00	184.28	13.34	40.02	26.68	98.28	15.12	18.90	-	-	-
10	364.07	256.64	190.99	113.40	126.74	100.06	34.02	34.02	26.46	-	-	-

Table 37. Results of a two-way analysis of variance to test the significance of intraspecific differences on the same trial (A) and differences between three trials (B).

N.S. - not significant to the 0.05 level

** - significant to the 0.05 level

*** - significant to the 0.01 level

Species	F Value (A)	Degrees of Freedom	Significance	F Value (B)	Degrees of Freedom	Significance
Leptasterias polaris	0.734	2, 18	N.S.	11.666	9, 18	***
Asterias vulgaris	2.877	2, 18	N.S.	10.770	9, 18	***
Crossaster papposus	0.769	2, 18	N.S.	1.837	9, 18	N.S.
Solaster endeca	7.600	2, 10	**	14.209	5, 10	***

Table 38. Results of a one-way analysis of variance to test the significance of interspecific differences in values of PC/R for the first trial.

** - significant to the 0.01 level

* - significant to the 0.05 level

N.S. - not significant to the 0.05 level

Species Combinations	F Value	Degrees of Freedom	Significance
L. polaris - A. vulgaris - C. papposus - S. endeca	33.30	3, 32	**
L. polaris - A. vulgaris	33.51	1, 18	**
L. polaris - C. papposus	61,96	1, 18	**
L. polaris - S. endeca	37.22	1, 14	**
A. vulgaris - C. papposus	6.38	1, 18	
A. vulgaris - S. endeca	2.35	1, 14	N.S.
C. papposus - S. endeca	1.09	1, 14	N.S.
A. vulgaris - C. papposus - S. endeca	3.97	2, 23	*

were highly significant. By examining the species-pair combinations, we see that most of this significant difference results from the highly significant differences between L.polaris and the other three species. Of the other three species-pairs, only A.vulgaris and C.papposus were considered to have a significant difference. The combination of A.vulgaris, C.papposus and S.endeca when considered together, however, showed significant differences. Since differences in comparison with L.polaris were considered significant all species were compared using a PC/R index (giving L.polaris a value of 1) and are listed in Table 41.

In conclusion, then, it can be stated that these species were found to vary significantly in pull capacities with L.polaris demonstrating the highest capacity and A.vulgaris, S.endeca, and C.papposus having successively lower values. Although all species cannot be proven to be significantly different, the indices are used as a guideline for morphological comparisons.

3. Reattachability

This term was coined to express mathematically the lessened pull capacity exhibited by a sea star after it has been pulled from the substrate. It expresses the pull capacity demonstrated during the second and third trials as a percentage of the first trial. Mean values of reattachability of each species are listed in Table 39.

A one-way analysis of variance to test whether any significant difference existed in the abilities of species to reattach was applied to the second trial data. No significant differences between species were noted (Table 40).

Table 39. Pull Capacity/Radius values of the second and third trials expressed as a percentage of the first trial (Reattachability).

	L. polaris		A. vulgaris		C. papposus		S. endeca	
Trial No.	2	3	2	3	2	3	2	3
Ind. # 1	68.5	86.6	32.5	33.8	20.0	20.0	57.6	24.2
2	141.4	55.3	35.1	47.3	68.8	131.3	40.0	10.0
3	69.7	60.1	83.0	36.2	58.3	75.0	67.4	56.5
4	66.0	19.1	10.5	2.6	20.0	20.0	65.7	94.3
5	90.1	45.1	29.1	19.8	1.8	1.8	63.4	54.4
6	46.2	22.4	17.9	17.9	200.0	375.0	61.4	42.1
7	45.3	29.2	82.3	41.2	150.0	200.0	-	-
8	64.6	22.2	88.3	64.7	133.4	264.7	-	-
9	274.0	89.0	300.0	200.0	15.4	19.2	-	-
10	70.5	52.5	111.8	88.2	100.0	77.8	-	-
Mean	93.6	48.2	79.1	85.2	76.8	118.5	59.3	46.9

Table 40. Results of a one-way analysis of variance to test the significance of interspecific differences in values of reattachability for first trials.

N.S. - not significant to the 0.05 level.

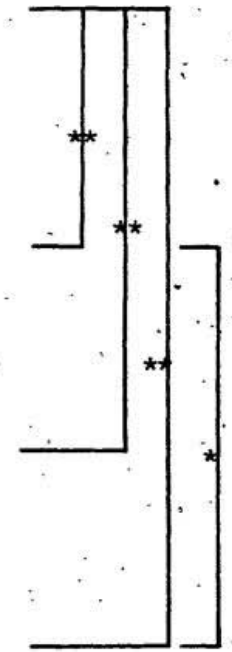
Species Pairs	F Value	Degrees of Freedom	Significance
L. polaris - A. vulgaris	0.177	1, 18	N.S.
L. polaris - C. papposus	0.307	1, 18	N.S.
L. polaris - S. endeca	1.440	1, 18	N.S.
A. vulgaris - C. papposus	0.004	1, 18	N.S.
A. vulgaris - S. endeca	0.314	1, 18	N.S.
C. papposus - S. endeca	0.393	1, 18	N.S.

Table 41. Summary of results of Pull Capacity experiments.

* - significant to the 0.05 level.

** - significant to the 0.01 level.

Species	P.C. (mean) 1st trial	P.C./R.	Significance	P.C. Index	Reattachability 2nd trial	Reattachability 3rd trial	No. of Non-testable Individuals
L. polaris	4122.10 (S.D. 1378.9)	440.6		1.000	77.3%	43.5%	2
A. vulgaris	1188.80 (S.D. 823.3)	141.8		0.322	46.7%	36.5%	4
S. endeca	1071.68 (S.D. 496.5)	85.2		0.193	61.6%	49.4%	1
C. papposus	388.39 (S.D. 461.4)	52.8		0.119	31.6%	45.1%	5
H. eschrichti	0.00	0.0	-	0.000	-	-	10



Hence, it can only be concluded that for each species, pull capacity decreases with the number of trials.

H-III Comparison of Morphological Features Affecting Pull Capacity

In Table 42 species are listed in decreasing order of pull capacity, with indices of PC/R recorded in brackets beside the species name. The morphological characters which may account for these pull capacity values are listed along the top.

The capacity of a sea star to secure itself to the substrate is dependent chiefly upon the podia or tube feet[1], i.e. the appendages of the water vascular system found along the oral surface of the rays and central disc. Podia are able to attach to the substrate by means of the terminal disc (or sucker) and/or by mucus secretion. Certain families (eg. Porcellanasteridae, Goniopectinidae, Astropectinidae, and Luidiidae) lack terminal suckers (Hyman, 1955), and hence, are dependent solely upon mucus secretion for attachment. Both families represented in the study area (Asteriidae and Solasteridae), however, are suckered and utilize mucus and suckers for attachment. Paine (1926) stated that 56% of the adhesive force employed by the podium was accounted for by sucker action, whereas, the remaining 44% was accomplished by other forces, chiefly the mucus.

Since all studied sea stars appeared to be similar in their mechanism for attachment, certain morphological features are considered which may account for the differing pull capacities of the species.

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[1]Attachment to the bottom can also be facilitated by cracks in a rocky substrate. A sea star which has forced itself into a crack may be held securely by its spines on the sides of the crack. Tube foot reliance for attachment would be lessened in this circumstance. This factor, however, is not considered in this discussion.

Table 42. Interspecific comparison of morphological characteristics governing the Pull Capacity of asteroids.

Figures in brackets are Pull Capacity Indices.

Species	No. of Rows of Podia	Skeletal Rigidity	Podia Used In Attachment	No. of Rays	R/r
L. polaris (1.000)	4	+++++	even	6	3.5 - 6.3 (Grainger, 1966)
A. vulgaris (0.322)	4	++	disjoint	5	3 (Gray et al, 1968)
S. endeca (0.192)	2	++++	even	9-13	2.3 - 3.3 (Grainger, 1966; D'yakonov, 1955)
C. papposus (0.119)	2	+	disjoint	9-13	1.7 - 2.7 (Grainger, 1966)
H. eschrichti (0.000)	2	+++	disjoint	5	3 - 4 (Grainger, 1966)

The following morphological features were considered:

1. Presence or absence of the terminal sucker. Since all are suckered, this character is simply included as a possible criterion when discussing other species.
2. Size and development of suckers. Since no histological work was performed during this study, no data can be presented; however, these factors should be considered in future discussion regarding attachment capacity.
3. Strength of podia (ie. presence or absence of spicules or connective tissue which may increase the tensile strength of a tube foot). Again, no data are presented because of lack of histological evidence.
4. Number and location of tube feet actually employed in attachment (see fig. 42). Since all tube feet are not utilized for attachment, the location and quantity of podia which are brought to bear during attachment is important.
5. Rigidity of skeleton. Because tube feet require a fulcrum and support to work against, this morphological character is considered important.
6. Number of rays. Since podia are found along the oral surface of each ray, the number of rays affects the total number of tube feet per individual.
7. Surface area of individual. It appears to be intuitively obvious that current action on a sea star would be proportional to surface area; however, inherent difficulties in measuring the surface area of an individual made it impossible to be considered in this study. Another parameter, the R/r ratio is a function of the surface area,

Figure 42. Drawings of Leptasterias polaris, Asterias vulgaris, Solaster endeca, Crossaster papposus, and Henricia eschrichti (oral surface) indicating the positions of the tube feet utilized in substrate attachment.

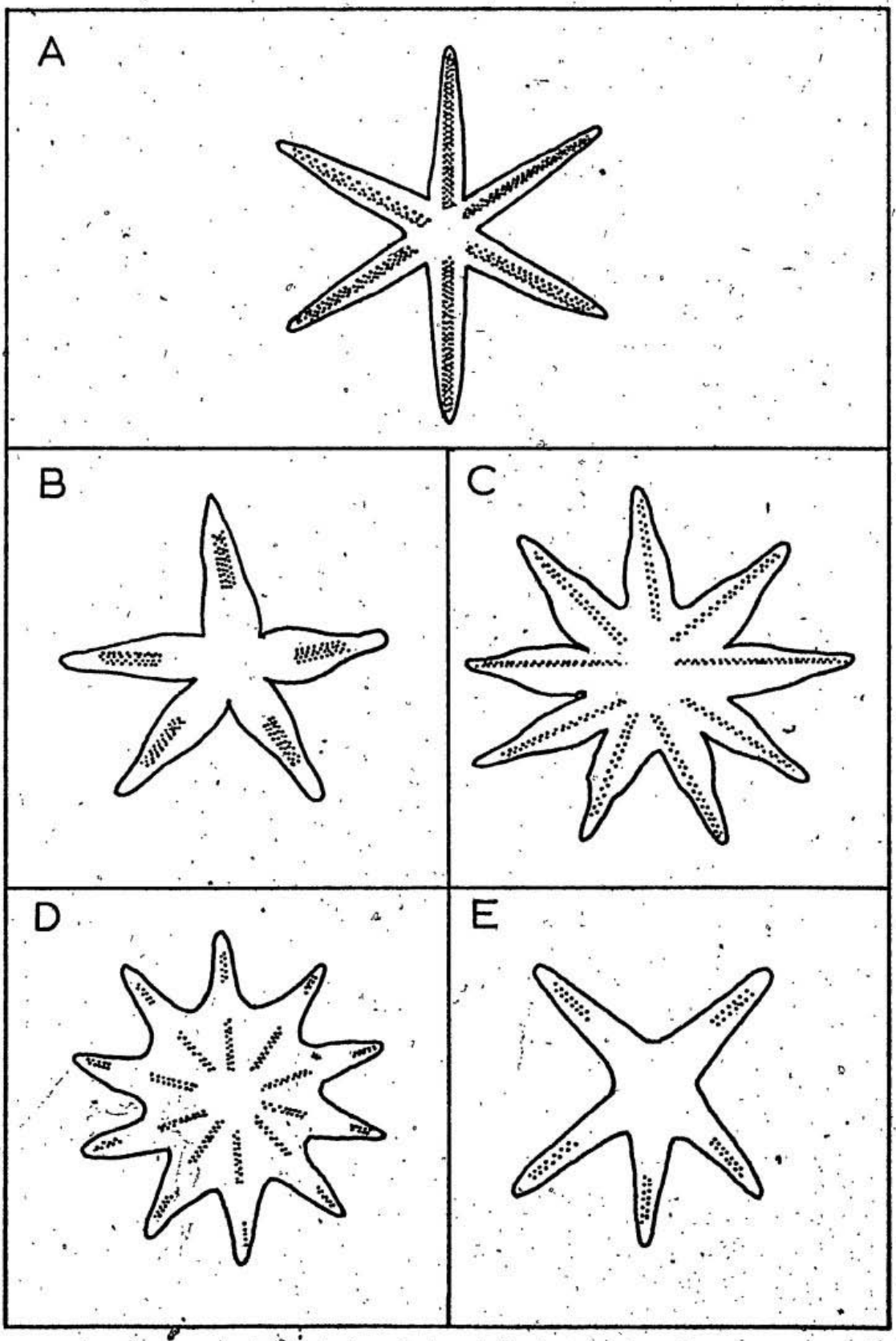
A - Leptasterias polaris

B - Asterias vulgaris

C - Solaster endeca

D - Crossaster papposus

E - Henricia eschrichti


A
B
C
D
E

and hence is utilized in this discussion. Since R is the radius of the sea star (ie. from the centre of the disc to the tip of the arm) and r is the radius of the disc, the smaller the R/r value, the greater the surface area. R/r values are listed in the summary of morphological features.

It appears evident that differences in pull capacities of the studied sea stars can be related to certain morphological features of each species. Difficulty arises in determining which of these characters are more important. Since L.polaris is superior to all these species in all of the morphological characters studied, except for number of arms, the number of arms possessed by a species appears to be relatively unimportant. This conclusion, however, can easily be refuted by stating that the superiority of L.polaris in all other features may counteract the lack of a high number of arms. Similiarly, L.polaris cannot be considered superior to A.vulgaris simply on the basis of having one additional arm, but on the basis of having a number of superior characteristics.

Logically, however, one would suspect the number of tube feet per unit area to be the most important criterion. Ideally, if the total number of tube feet per individual and the surface area of that individual were known, species could be compared directly without having to compensate for the number of arms, the number of tube feet in a row, and the relative size of the central disc. Since no published values exist concerning the number of tube feet per surface area, these morphological characters have to be considered individually.

Unfortunately, in order to test this hypothesis, one would have to have a greater number of species demonstrating a low value in one characteristic and a high value in another characteristic.

The unmeasurable pull capacity of H.eschrichti introduces further considerations. The major hindrance here appears to be a size factor. The difficulty of obtaining specimens of small size of all other species for comparison made it impossible however, to test this hypothesis. Again, although size may be a factor, the low number of tube feet, the low number of arms, and position of tube foot attachment also may affect its pull capacity.

In general, then, a large number of morphological characteristics exist which may account for the varying capacities of species to resist a pull. Apart from the number of tube feet per surface area unit, no one factor can be considered most important. L.polaris demonstrates a pull capacity exceeding all other species by a multiple of three because it has a number of characteristics which are superior to those possessed by the other species. Pull capacities vary to a lesser extent between the remaining species because of small variations in the criteria which were examined. A more detailed study of pull capacity with respect to morphological characteristics is required to elucidate this relationship more fully.

I. Intraspecific and Interspecific Behavioural Reactions

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I. Intraspecific and Interspecific Behavioural Reactions

I-I Introduction

Although extensive studies have been performed to determine the responses of various invertebrates to the contact or presence of sea stars, few workers in this field have examined the responses of sea stars to each other. In summarizing responses to sea stars, Feder and Christensen (1966), list only two references to interactions between sea stars, both unpublished. Recently, Castilla and Crisp (1970) and Feder (1967) have examined the responses of A.rubens to C.papposus and S.endeca.

Several authors, (Feder and Lasker, 1964; Feder and Arvidsson, 1967; and Mackie, 1970) have been active in trying to determine the substance responsible for causing avoidance or escape responses to sea stars. In addition, Castilla & Crisp (1970) and Castilla (1972), have attempted to establish evidence for an olfactory sense in sea stars. Methods of observation varied, Feder observing responses between contacted or proximal animals, and Castilla observing responses of A. rubens to C.papposus by utilization of a Y-maze.

In the present study, sea star responses were examined in a two-fold manner, firstly by examining the proximity of sea stars to each other, and secondly, by observing responses when sea stars were brought into contact with each other. These results are considered on the basis of predator-prey and competitive relationships and their effect on the local distribution of each species.

I-II Materials and Methods

Proximity studies were carried out in both the laboratory and the field, whereas contact responses were considered only in the laboratory. Since each method involved differing observational techniques, each method is presented separately.

I-II.1 Proximity Studies

Aggregations observed during diving were examined to determine the species involved, relative abundance, and possible activity of the aggregated individuals, whereas laboratory investigations centred around observations of individuals under a variety of abundances and species diversities in the wet tables and tanks of the M.S.R.L. Special note was made of those species which were either in close proximity or in contact with each other. Attempts were made to cause aggregations by providing food or suitable substrates. Observations of physical factors apparently causing aggregations of individuals in certain areas of the tanks were also recorded.

I-II.2 Contact Experiments

Observations of contact between sea stars maintained in the laboratory were made while sea stars were engaged in a variety of activities such as feeding, 'resting',[1] and moving.

In testing responses of 'resting' and feeding sea stars, the arm of one sea star (the contacting individual) was brought into contact

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[1] A 'resting' star was defined as any sea star which was not moving and was either firmly attached to the substrate by its tube feet or had tube feet in the contracted position. In this position, the oral surface of the sea star was flush with the substrate.

with an arm of a 'resting' or feeding sea star (the contacted individual). All species-pair combinations of resting individuals were tested, but only the responses of feeding A.vulgaris, L.polaris, S.endeca and C.papposus individuals were examined.[1] In all cases, only the responses of the contacted sea star were noted. Each interaction was tested a minimum of five times, recording those species-pairs which responded consistently. If varied responses were observed for the same species-pair, further testing was carried out to determine which response occurred most frequently. If an alternate response occurred between 20 and 40% of the time, it was recorded as an occasional response.

I-III Results

I-III.1 Proximity Studies

I-III.1 (i) Diving Observations

With the exception of S.endeca, all remaining species were observed in aggregations. These aggregations varied in degree of contact, number of individuals, and species components. For the most part, aggregations where individuals came into close contact were monospecific, and aggregations where contact was reduced were multispecific. Of all the studied species, A.vulgaris had the greatest tendency to aggregate, occasionally forming clumps of over 50 individuals. Aggregations of closely packed individuals often formed around food

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[1] H.eschrichti and Henricia sp. were not considered because of the difficulty in determining when they were feeding.

material such as dead fish. Even though L.polaris was often near such clumps it did not engage in the aggregation. In large feeding aggregations, individuals (A.vulgaris) were commonly piled on top of one another. Individuals touching the prey were directly feeding with their stomachs extruded onto the surface of the prey. Individuals not touching the prey often were observed with their stomachs extruded although they had no access to the prey itself. Aggregations involving A.vulgaris also occurred in areas of protection from water disturbance. Contact was usually lateral and often L.polaris was observed in this type of aggregation.

Feeding aggregations of L.polaris were not as commonly observed as those of A.vulgaris and often involved lower numbers of individuals. Contact with the prey appeared to be essential in these clumpings. Brooding aggregations of L.polaris were more difficult to assess. The amount of contact was minimized, and yet abundance appeared to be concentrated in certain areas during the spawning and brooding period (note observations at Bay Bulls, section F-III.2(iii)).

Aggregations of Henricia appeared to result not from mutual attraction of individuals, but from attraction to certain current-producing substrates such as the yellow sulphur sponge, Halichondria panicea, or the encrusting tunicate, Didemnum albidum. On these substrates, often large aggregations of individuals were observed, predominantly composed of the more abundant H.eschrichti. The presence or absence of Henricia sp. did not appear to be detrimental or beneficial to aggregation formation. Contact in these aggregations was minimized

and density appeared to be regulated by local Henricia abundance rather than by available space on the current-producing substrate. While both species were observed on both types of substrate, Henricia sp. was observed more frequently on sponge substrate, and H.eschrichti more frequently observed on D.albidum.

C.papposus was observed mostly singly; however, high abundances of this species were observed occasionally within relatively small areas. In November 1969, one concentration was observed at a depth of approximately 80 feet. No contact was present between the eight adjoining sea stars which had gathered in an area approximately 2 square meters in size. Feeding and reproduction were ruled out as causes of this concentration.

S.endeca was never observed in aggregations in the field; however, low density may have been a determining factor.

I-III.1 (ii) Laboratory Observations

Aggregation formation in the laboratory appeared to result from one of three factors; mutual attraction to prey (or current-producing substrates in the case of Henricia), responses to physical or chemical aspects of the holding tanks, or overcrowding.

Responses during feeding were varied and species-dependent. Only individuals belonging to the species A.vulgaris, L.polaris, H.eschrichti and Henricia sp. were observed feeding on the same prey item simultaneously with another member of the same species.

As in the field, A.vulgaris demonstrated the greatest capacity in this respect, whereas, L.polaris adopted this condition only when the prey item was large, in short supply, or following a period of starvation.

Laboratory observations confirmed the attraction of Henricia to sponge[1] (reported in section E-V.1) and demonstrated that individual Henricia would feed while in close proximity. Contact in this type of 'feeding aggregation' was minimized, and there appeared to be no species distinction between H.eschrichti and Henricia sp. in the reaction of individuals to each other.

Neither C.papposus nor S.endeca were observed feeding on the same prey item; however, observations of more than one S.endeca attacking a sea cucumber, Cucumaria frondosa, were frequent. After capture, however, only one individual remained to feed. C.papposus adopted a strictly 'lone wolf' feeding strategy.

Of those species that participated in feeding aggregations, only the pairs L.polaris, and A.vulgaris, and H.eschrichti and Henricia sp. were observed feeding in dispecific feeding clumps. Whenever mixed species feeding aggregations occurred between A.vulgaris and L.polaris, a small number of individuals were involved. Based on a large number of observations of these species in the laboratory under a variety of conditions (such as varied abundance, species proportions, environmental parameters, physiological conditions of asteroids, and conditions of starvation), mixed feeding aggregations occurred only when the number of A.vulgaris in the clump equalled or was less than two. The number of L.polaris in the clump appeared to be insignificant, although aggregations of L.polaris never exceeded four. Hence, only the aggregations listed in Table 43 were possible.

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[1] Since difficulties were encountered in obtaining whole D.albidum, this experiment could not be repeated using this species.

Table 43. Numbers of Asterias vulgaris and Leptasterias polaris observed in dispecific aggregations.

Number of *Asterias vulgaris*	Number of *Leptasterias polaris*
1	1
1	2
1	3
1	4
2	1
2	2
2	3
2	4

In conditions of overcrowding, various degrees of aggregation formation occurred depending on space, the species components, and physical and chemical factors.

If large numbers of L.polaris and A.vulgaris were placed in a tank without water movement, a greater degree of contact took place between members of the same species. Often centres of abundance of each species occurred with contact of individuals of differing species taking place around the perimeter of these centres of abundance. With water movement, this pattern became more clearly defined, L.polaris gathering in areas of high current, commonly to the complete exclusion of A.vulgaris, and A.vulgaris gathering where currents were minimal.

If the sea star predators, S.endeca and C.papposus, were added to this large mixed population of A.vulgaris and L.polaris, aggregation formation of A.vulgaris was increased with individuals piled on top of each other. Such extreme close packing by L.polaris was not observed. Around C.papposus a space free of other sea stars formed, commonly with L.polaris as its nearest neighbour. S.endeca was not surrounded by such a large free space and frequently contact was observed between S.endeca and L.polaris.

If a mixed population of H.eschrichti and Henricia sp. were placed together in a tank, aggregations often occurred in areas of shade and/or low water disturbance.

I-III.2 Contact Experiments

Responses of individuals varied with the species involved in the contact interaction, and the nature of the activity.

Observations of moving sea stars were the most difficult of the three (ie. feeding, 'resting', and moving) activities to interpret. In general, moving sea stars tended to avoid each other independently of the species of the two confronting individuals. However, such a large array of interactions existed in this activity, that no definite conclusions regarding interspecific reactions could be reached.

Individual sea stars responded in a more or less consistent fashion when another sea star was brought into contact with them during feeding or 'resting' activities. These responses can be divided into three catagories: contact response, avoidance response, and escape response. Contact responses were exhibited by all sea stars regardless of whether any further response was exhibited whenever two sea stars were brought into contact. The nature of the contact response varied slightly between species, but common characteristics of this response were the movement of the fine podia on the distal portion of each arm (usually the arm or arms opposite the contacted arm beginning movement initially), followed by the raising up of the body off the substrate brought about by the expansion of the rest of the tube feet. When avoidance responses were observed, the contacted sea star moved the arm which was in contact with the sea star so as to avoid contact. In some cases, movement of more than one arm was observed, occasionally accompanied by a slight movement of the entire body of the sea star to a position a short distance away from the contacting species. Escape responses were simply an extension of the avoidance response with the result that sea stars moved rapidly away from the contacting sea star, continuing movement until a considerable

distance separated them.

Tables 44 and 45 list the most frequently observed responses of contact interactions between members of the same and differing species.

The latency of the response of the contacted individuals varied with the species. (Tables 44 and 45 list the species in descending order of latency). In general, avoidance and escape responses were more delayed in the feeding condition than in the resting condition, possibly resulting from either the hesitation of a sea star to leave a captured prey item and/or the process of withdrawing the stomach into the body cavity. Only slight differences in the type of response were noted for sea stars which were engaged in feeding or resting. These differences appear to be mostly associated with individuals competing for the same food resource. C.papposus elicited escape responses in resting C.papposus; however, feeding C.papposus never moved away from prey. Similarly, S.endeca did not avoid or move away from C.papposus or other S.endeca when they were feeding, but would occasionally when they were resting. The response to S.endeca, a predator of A.vulgaris, was also dampened when the A.vulgaris was feeding (ie. only occasionally did A.vulgaris exhibit an escape response to S.endeca while feeding).

In general, escape responses were associated with the predator-prey relationship. C.papposus, an active and voracious predator of sea stars, elicited escape responses in all species. Similarly, S.endeca, a less active sea star predator, elicited escape responses in A.vulgaris, H.eschrichti and Henricia sp. One exception was the response of L.polaris to S.endeca. In both feeding and resting activities, no response beyond an initial contact response was noted.

Table 44. Interspecific and intraspecific responses observed when an asteroid is brought into contact with a resting asteroid.

C.R. - contact response

A.R. - avoidance response

E.R. - escape response

Contacted (Resting) Species	Contacting Species					
	A. vulgaris	C. papposus	L. polaris	H. sp.	H. eschrichti	S. endeca
Asterias vulgaris	C.R.	E.R.	C.R. (A.R.)	C.R.	C.R.	E.R.
Crossaster papposus	C.R.	E.R. (A.R.)	C.R.	C.R.	C.R.	A.R.
Leptasterias polaris	C.R. (A.R.)	E.R.	C.R.	C.R.	C.R.	C.R.
Henricia sp.	C.R.	E.R.	C.R.	C.R.(A.R.)	C.R.(A.R.)	E.R.
Henricia eschrichti	C.R.	E.R.	C.R.	C.R.(A.R.)	C.R.(A.R.)	E.R.
Solaster endeca	C.R.	A.R. (E.R.)	C.R.	C.R.	C.R.	C.R.(A.R.)

Table 45. Interspecific and intraspecific responses observed when an asteroid is brought into contact with a feeding asteroid.

C.R. - contact response

A.R. - avoidance response

E.R. - escape response

Contacted (Feeding) Species	Contacting Species			
	A. vulgaris	C. papposus	L. polaris	S. endeca
Asterias vulgaris	C.R.	E.R.	C.R.	C.R. (E.R.)
Leptasterias polaris	C.R. (A.R.)	E.R.	C.R.	C.R.
Crossaster papposus	C.R.	C.R. (A.R.)	C.R.	C.R.
Solaster endeca	C.R.	C.R.	C.R.	C.R.

Interactions between sea stars competing for the same food resource were varied. Except for C.papposus, the most frequent intraspecific response was merely a contact response. Occasionally H.eschrichti, Henricia sp. and S.endeca elicited avoidance responses. The most pronounced aversion to individuals of the same species was showed by C.papposus. Escape responses were most commonly observed and the less averse avoidance response was observed occasionally between individuals of this species. Of the competing species-pairs, ie. L.polaris and A.vulgaris, S.endeca and C.papposus, and H.eschrichti and Henricia sp., avoidance responses were only occasionally observed except between C.papposus and S.endeca where avoidance and escape responses were very frequent.

Species which were not either associated by competition or by the predator-prey association did not respond to each other beyond the contact response.

I-IV Discussion

Numerous examples of evidence that sea stars are attracted to food material by an olfactory sensitivity are reported in the literature. Reviews of this phenomenon are reported in Feder and Christensen (1966), and more recently in Castilla and Crisp (1970). Since distance and chemical gradient appear to be important in this mechanism, contact between tested animals was utilized as an experimental criterion to ensure that every tested individual received maximum stimulation from any chemical released from a contacting sea star.

Mackie (1970) has shown that escape responses elicited by marine

invertebrates result from the secretion of surface-active agents by predatory sea stars. This secretion, partially purified by Feder and Lasker (1964) and purified by Mackie, Lasker and Grant (1968), has been shown to be a steroid glycoside (Mackie, 1970). It would appear highly probable that a similar mechanism of olfactory response to some surface-active agent is responsible for the contact, avoidance, and escape responses demonstrated by sea stars in response to other individuals.

As we have seen in the contact experiments, sea stars respond differently to each species indicating that the steroid glycoside produced by sea stars must be specific,[1] enabling sea stars to distinguish between a predatory species, a competing species, or a non-competing, non-predatory species.

The evolution of behavioural responses appears to be related to both the predator-prey association and the competitive species relationship. An escape response to a predator is an obvious example of an adaptation for survival. One puzzling exception to this hypothesis is the response of L.polaris to S.endeca. Since S.endeca is a predator of L.polaris, we would expect similar responses as elicited in A.vulgaris, H.eschrichti and Henricia sp., or a similar response as that evoked in L.polaris by C.papposus. If we assume that L.polaris has not yet evolved an escape response because of insufficient confrontation in the environment, we again encounter a difficult roadblock. The abundance-distribution patterns of S.endeca and L.polaris overlap more

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[1] One exception to this rule appeared to apply to H.eschrichti and Henricia sp. No differences in response were noted interspecifically or intraspecifically.

than those of S.endeca and A.vulgaris. The converse hypothesis is tenuous but may have some validity. Owing to its long time association with S.endeca and C.papposus, L.polaris may be able to better distinguish between the steroid glycosides of these species than can A.vulgaris, H.eschrichti and Henricia sp. If we assume that the predator pressure exerted by S.endeca on L.polaris is very low, a situation of continual confrontation between individuals of these species may occur without S.endeca attempting to prey on L.polaris; hence, an escape response may not have evolved.

Avoidance responses, ie. those shown by competitive species, may have the effect of separating the spatial niches of the species involved. The actual effect of this occasional response shown by competitors appears to affect distribution interspecifically only on a microscale. For example, this response appears to affect aggregation formation but is not effective in excluding one species from the 'preferred habitat range' of another. A more detailed study of various habitats with differing exposure, temperature, oxygen and salinity gradients, and substrate, etc, may show this competitor interaction to be more important in excluding one species from a habitat to which its competitor is slightly better adapted.

Intraspecifically, avoidance and escape responses would appear to be factors in allowing species such as C.papposus and S.endeca to adopt a lone wolf feeding strategy, and in allowing species such as A.vulgaris, L.polaris, H.eschrichti and Henricia sp., to feed collectively with members of their own species.

Concerning escape responses related to the predator-prey

relationship, we have noted previously that L.polaris and A.vulgaris have decreased abundances in the areas of maximum abundances of C.papposus and S.endeca. One would be naive to suggest that this distribution pattern is the direct result of this relationship rather than a multifactorial causation; however, decreased abundance caused by predation plus a pronounced escape response may be very dominant factors in formation of distribution patterns in specific areas. The key to an understanding of this relationship may be the motility of a specific species. From spatial abundance-distribution patterns, we have seen that H.eschrichti, a sluggish species, inhabits areas overlapping with the greatest abundance of its predator. Since its ability to escape C.papposus and S.endeca is very poor, population density may be regulated in part by predation by C.papposus and S.endeca, rather than a specific effort to emigrate from areas populated by a predator. On the other hand, A.vulgaris, an elusive, extremely motile prey of C.papposus, may avoid areas of high C.papposus abundance.

The possible effect of C.papposus and S.endeca on brooding location of L.polaris has already been discussed in the section F-V.1, but bears repetition here. Brooding female L.polaris exhibiting an escape response to the predator would abandon eggs; hence, aggregation of brooding females would tend to develop in predator-free areas causing centres of abundance due to the addition of juvenile sea stars.

In summary, we can say that the evidence of interactions between sea stars has an apparent visible effect on the microdistribution of sea stars (chiefly aggregation formation), but conclusions regarding the overall distribution patterns are merely speculative.

J. Laboratory Light Preference Experiments

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J. Laboratory Light Preference Experiments

A series of experiments was undertaken to determine whether sea stars are capable of selecting a specific intensity of light given a choice of three light levels.

J.I. Materials and Methods

The experimental apparatus consisted of four tanks mounted in series side by side on wooden frames. Tank units were physically separated from each other by a wall of plywood and covered above and on all sides by opaque black plastic to prevent light penetration. A flap of black plastic covering the front of each tank unit allowed the experimenter access to the tanks. Suspended above the tanks within each tank-unit were two light bulbs, covered by a conical shield and spaced exactly one-third of the distance from the ends of the rectangular tanks (2½' X4').

In each tank-unit, the bulbs were of equal wattage but the wattage of the bulbs varied from tank one through tank four. Table 46 shows the wattage of the bulbs in each tank and the values of relative irradiance measured using the Martex R.I. meter along the bottom of each tank. The R.I. meter was also used to determine whether the intensity of light over the bottom of each tank[1] was equally distributed.

Tanks were fitted with screens which divided the length of the tank into three light regions of equal size (one-third being open (100%) illumination, one-third being screened (50%)[2] illumination, and one-third being covered (0%) illumination)).

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[1] By use of the R.I. meter, the intensity of the 100, 60, and 25 W bulbs were expressed as a percentage of the 150W bulb.

[2] Again, by use of the R.I. meter, various screen types were tested until a screen which allowed one-half the light intensity of the open area to be transmitted was found.

Table 46. Relative irradiance monitored in tanks one to four for light preference experiments.

Tank	Wattage	Relative Irradiance (%)
1	150	100
2	100	55
3	60	20
4	25	10

After each tank had been filled with ambient sea water to a depth of 2¼", the outflow pipe was removed and replaced with a No. 12 rubber stopper so that there was no movement of water in the tank. The removal of the overflow pipe assured that the particular section of the tank where it is normally found was now of a size and area equal to the other two.

Experiment No. 1

In each tank, 15 A.vulgaris[1] of approximately the same size (size range 5 - 7 cm. in radius) were placed oral side up along the midline[2] of the tank. The black plastic flap of each tank was put in place over the end and sealed with tape along the edges. After a time interval of 60 minutes, the flap was lifted and the number of sea stars in each light-level area was counted and recorded. A sea star was considered to be within a light-level area if at least three rays and a portion of the central disc were located in that area.

After the distributional count was completed, the sea water was drained out of each tank and again filled to the previous 2¼" level. The procedures were repeated for eight trials.

Experiment No. 2

Using the same procedures as in Experiment No. 1, light-level preference of L.polaris was studied. These specimens were also collected at Bay Bulls.

Experiment No. 3

Since large quantities of S.endeca and C.papposus could not be

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[1] These specimens were collected December 8, 1970 at Bay Bulls.

[2] Midline refers to an imaginary line which divides the length of the tank into two equal halves.

collected, only 15 specimens of C.papposus and 3 specimens of S.endeca were observed under experimental procedure No. 1. Initially 15 C.papposus were placed in tank No. 3 and three S.endeca placed in tank No. 4 for trial one. Specimens were transferred to tanks Nos.1, 4 for trial two, Nos.2 and 3 for trial three and No's.1, 2 for trial 4.

All the specimens in experiment No. 3 had nine rays; hence, a sea star was considered to be in a given area if at least five of its arms were observed in that area.

J-II Results

Four basic assumptions were made in statistically analysing the results of these experiments.

1. Movement from the mid-line of the tank was random, i.e. an equal number of sea stars are assumed to move away from the mid-point in either direction.

2. Any result differing from random expectation demonstrates both the ability of sea stars to detect a difference in light intensity, and an ability to select a preferred light level.

3. Any sea stars found in the open area of the tank are assumed to have moved there because they have made a selection between 50% illumination and 100% illumination. Similarly, any sea star found in the covered section, had made a decision between 50% illumination and 0% illumination.

4. Sea stars found in the screened area at the end of a trial may demonstrate a preference for 50% illumination over 100% illumination and/or 0% illumination, or it may simply indicate no movement and no decision on the part of the sea star.

Only the number of sea stars that moved into either the open or the covered areas were considered. A chi-square test was applied to these data considering the expected value to be one-half of the total number of individuals displaced from the screened area.

As shown by Table 47, a greater proportion of individuals of each species in all tanks moved towards the area of greatest illumination. Clearly, differences existed between the responses of the four species to light. L.polaris displayed the strongest positive movement towards the open area of all the studied species. This phototactic response was greatest at the highest light intensity (tank 1). A.vulgaris demonstrated a non-uniform reaction to light for the four light intensities. At high light intensity (tank 1), very little preference was shown for the open area, whereas, in tank 3 (approximately 20% of the intensity of tank 1), a highly significant (to the 0.01 level) positive phototaxis was recorded. Intermediate levels of phototactic response were displayed for tanks 2 and 4.

Although C.papposus did not demonstrate significant differences in movement between the two areas, they nonetheless displayed a positive attraction to the more highly illuminated area. A 91.3% probability existed that C.papposus in tank 3 (20% illumination of tank 1) was more attracted to the open area than to the covered area. Lower probabilities in decreasing order were recorded for tanks 2, 1, and 4.

Also, for S.endeca, a greater number of individuals moved to the high intensity area than moved to the zero intensity areas; however, a low value of significance was calculated for this ratio.

Table 47. Chi square analysis of light preference experiments.

** - significant to the 0.01 level

* - significant to the 0.05 level

N.S. - not significant to the 0.05 level

Species	Tank No.	Illumination 100%	Illumination 0%	Degrees of Freedom	χ^2	Probability	Significance
L. polaris	1	119	1	11	58.20	0.999	**
	2	94	7	11	39.06	0.999	**
	3	94	8	11	38.74	0.999	**
	4	92	7	11	38.84	0.999	**
A. vulgaris	1	46	30	7	7.05	0.576	N.S.
	2	58	26	7	11.01	0.862	N.S.
	3	67	17	7	18.57	0.990	**
	4	60	14	7	16.56	0.980	*
C. papposus	1	12	1	2	3.73	0.845	N.S.
	2	18	4	2	4.67	0.903	N.S.
	3	16	3	2	4.88	0.913	N.S.
	4	12	6	2	1.50	0.528	N.S.
S. endeca	all	6	3	5	2.50	0.224	N.S.

J-III Discussion

Difficulty exists in trying to relate observations of animal responses under controlled laboratory conditions to how organisms actually behave in their natural environment. An experiment such as this one in which all parameters save one (light) are held constant shows how sea stars respond to the specific conditions of the experiment, but not how an organism responds to this parameter in its environment. In the case of light, it would be next to impossible to duplicate in the laboratory, the continuum of light conditions such as the periodicity, range, intensities, and spectral frequency to which sea stars are exposed in their natural environment. In this experiment, the responses of sea stars were examined when they were confronted with an actual boundary between two areas of different light intensities. In the habitat of sea stars, this circumstance exists whenever there is a shadow formed by rocks, algae, or other aspects of the topography such as steep slopes and caverns in the rock face. Such major light intensity changes do not occur in the same distance (as in the experiment) as a result of depth changes.

The phototactic responses of sea stars as shown by this experiment do not lead directly to the conclusion that the studied species of sea stars will seek shallower water because of the higher light intensity found in that location. However, the following conclusions are considered valid interpretations of the results:

1. All species did not respond equally to each level of intensity.

L.polaris showed a highly significant phototactic response at all light intensities; however, greatest responses were found at the highest intensities.

A.vulgaris showed significant responses in tanks 3 and 4 where light intensity was low, whereas, a weaker phototactic response was shown in tanks 1 and 2 where higher intensities of light existed. This response appears to indicate that A.vulgaris has a varied response to light depending on intensity.

Both C.papposus and S.endeca demonstrated lesser degrees of attraction to light.

2. These experiments showed aversion to darkness, indicating that most of the studied species of sea stars would avoid shaded areas such as caverns or the underside of rocks. Additional weight is given to this conclusion by underwater observations which indicated that only S.endeca, H.eschrichti,[1] and young A.vulgaris[2] were found in such shaded areas.

3. Sea stars are capable of detecting differences in light intensity and show preference for specific intensities.

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[1] Difficulties existed in testing the response of H.eschrichti to light using this experimental apparatus. Individuals of this species demonstrated an insufficient amount of mobility to react to the various levels of light. Hence, problems of temperature regulation and possible light adaptation entered into experimental error when extended periods of time (greater than five hours) were required. After several unsuccessful trials of long duration, this aspect of light response was judged to be better considered from field observations.

[2] No adult A.vulgaris were found under rocks or other areas of shade, whereas young were often found in these areas indicating a change in response to light with increased size.

K. Substrate

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K. Substrate

K-I Introduction

Since the substrate within the study area was uniform, this parameter of the environment could not be quantitatively assessed as affecting sea star distribution. However, it is possible to comment on the sand substrate at the bottom of the cliff area as being a factor limiting asteroid distribution.

During the study, casual observations of this area were made at the end of every photographic survey.

K-II Results

Only two species, A.vulgaris and S.endeca, were noted on this bottom. S.endeca, as previously noted, moved onto this substrate while pursuing a prey species and moved off shortly after ingestion had taken place. A.vulgaris was occasionally observed on the sand but always within five meters of the rock face. At another locale, Bellevue Beach, A.vulgaris was observed on a sand-mud bottom which was characterized by an abundance of M.edulis.

K-III Discussion

The absence of sea stars from this substrate can be explained on the basis of a number of other parameters in addition to solely the nature of the substrate. Two factors, which also are considered limiting and are characteristic of the sand bottom, are occasionally high water disturbance and lack of prey. It was speculated that during storm conditions, a strong current moves along this sand bottom in a north-easterly direction. Sea stars would have difficulty attaching themselves to a shifting, particulate bottom, and could be swept away from this area.

Galtsoff and Loosanoff (1939) noted that A.forbesi was found on all substrates having molluscs and hence, the lack of prey in this area may be a limiting factor for A.vulgaris.

In discussing substrate as being an important characteristic of the habitats of sea stars as a group, Grainger (1966) lists C.papposus as being found on all types of substrates (including sand bottoms), but preferring hard bottom substrates, and L.polaris, S.endeca and H.eschrichti as never being found on substrates which are composed entirely of sand, but preferring substrates which have rock as a component[1] (ie. mud-rock, rock-sand, and rock-gravel). Hence, the nature of the substrate may act as a barrier for movements of S.endeca, L.polaris and H.eschrichti but A.vulgaris probably avoids the sand bottom because of lack of prey on this substrate.

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[1]He also lists L.polaris as being found occasionally on mud bottoms.

page 247 does not exist

General Discussion

At any point in time, the distribution and abundance of a species can be defined by the space it occupies. Since this space has physical boundaries, we can simply define its location by a system of reference points on a map. If we stop our investigation at this point, we can define the space which a species occupies, but we have no conception of why it is found only in this location. The next approach then, is to further define the space occupied by the species in terms of its unique features. In other words, we are answering the question: what makes this area unique enabling a species to live in this space? Hence, we embark on a systematic study of any parameter of this environment which varies with space or location. We discover at this point, a number of disturbing facts.

Firstly, we find that there are an almost infinite number of physical, chemical, and biological parameters which can describe this space. Secondly, if we examine each parameter individually, we find very few physical and chemical parameters that are individually unique here. At this point, we make the assumption that the distribution of a species is dependent not upon the distribution of any one of these parameters, but upon the unique combination of parameters characteristic of its living space. The problem seems monumental because we are again aware that an almost infinite number of parameter combinations can define this space. To solve this problem, we adopt a different approach. We have noted that within the living space of a species, its abundance is not uniform. There are areas of high density, areas of moderate density, and areas of low density. We decide to examine

what parameters vary with the distribution pattern of the species. After this study, we find that we were able to discover a number of characteristics of the environment whose gradients correlated in some way with the abundance-distribution patterns of the species. In considering these factors, though, we still find ourselves with many unanswered questions such as:

Do the parameters that we have correlated with the distribution of the species actually have an effect on their abundance-distribution patterns? If so, how do they effect the patterns?

In order to answer these difficult questions, we must examine the interaction of the environment with the specific biological characteristics of the species involved, and in turn establish how these interactions affect the population dynamics of the species and regulate their distribution and abundance. The following model (fig. 43) is proposed to deal with these interactions.

Components of the Model

A. Environmental Parameters

Within the marine environment, a large number of parameters exist which may affect the abundance and distribution of a particular species. In order that the number of parameters did not exceed the practical limitations of this study, only those which were suspected[1] to affect directly or indirectly the physiological processes essential for life of sea stars or effect the sensory receptors of a sea star were considered.

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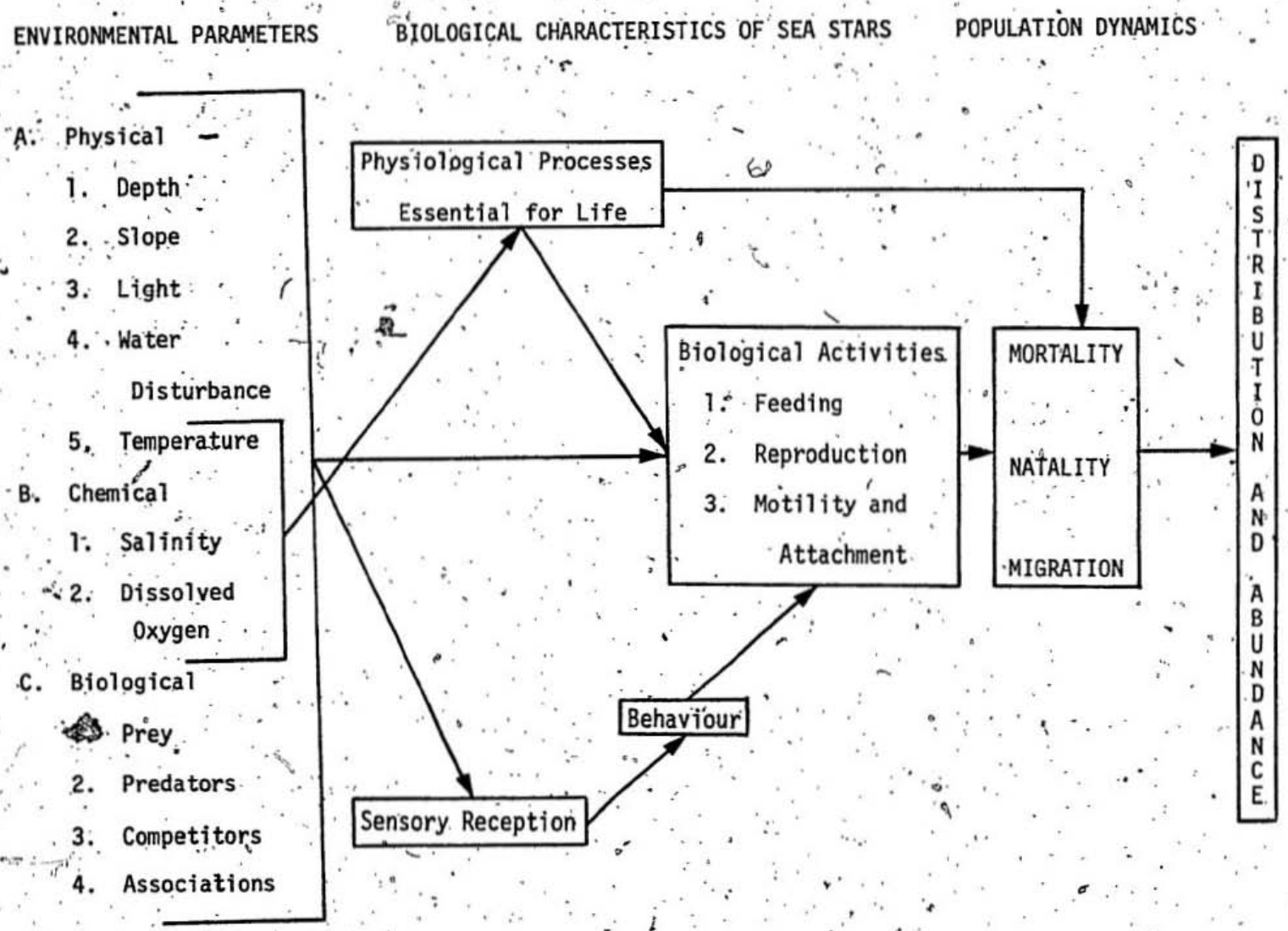
[1] Parameters were suspected to be involved in these relationships if either they had been previously mentioned in the literature pertaining to sea stars as having an effect, or if a possible relationship was uncovered during the pilot study.

Figure 43. Hypothetical model presenting the interrelationships of factors and processes regulating the distribution and abundance of sea stars.


ENVIRONMENTAL PARAMETERS
BIOLOGICAL CHARACTERISTICS OF SEA STARS
POPULATION DYNAMICS
A. Physical
1. Depth
2. Slope
3. Light
4. Water Disturbance
5. Temperature
B. Chemical
1. Salinity
2. Dissolved Oxygen
C. Biological
1. Prey
2. Predators
3. Competitors
4. Associations
Physiological Processes Essential for Life
Biological Activities
1. Feeding
2. Reproduction
3. Motility and Attachment
Behaviour
Sensory Reception
MORTALITY
NATALITY
MIGRATION
DISTRIBUTION AND ABUNDANCE

Several factors were also excluded because they did not directly apply to the study area. Examples of these parameters are substrate[1], air-water interface characteristics, and chemical pollutants. Detailed water chemistry parameters were also excluded because of lack of equipment for analyses.

B. Physiological Processes Essential for Life

Obviously, a large set of processes is inherent in this multi-dimensional parameter. Such processes would include regulatory mechanisms, nutrition, gaseous exchange, metabolism, excretion, ionic and osmotic balance, and transport mechanisms. In general, any characteristic dependent upon the external environment which would affect the ability of an organism to survive is included.

C. Sensory Reception

Items considered in this component would be any type of receptor that the organism has for detecting gradients in environmental parameters. Examples of types of receptors are photoreceptors, chemoreceptors, temperature receptors, mechanoreceptors, and pressure receptors. Included in the present model, however, are sensory receptors specifically possessed by sea stars.

D. Behaviour

Included in this component would be any response that organisms have to elements of the environment that would ultimately affect the probability of survival of the organism.

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[1] Uniform substrate, i.e. rock, was selected for the study area.

E. Biological Activities

The items chosen for this component are activities that a sea star would carry out within its habitat which would ultimately affect the probability of its survival. Activities chosen for this component were (i) feeding, (ii) reproduction, and (iii) motility and attachment.

F. Population Dynamics

Factors selected for this component were those that would cause a change in the distribution and abundance of a species. For the purpose of this theoretical discussion, only mortality, natality, and migration are considered.

General Pathways

Before considering how each factor of the environment interacts with the biological characteristics to ultimately affect the distribution and abundance patterns of a particular species, we must establish the nature of the interactions and the mechanisms and possible effects of each pathway of the model.

Initially there are two ways by which the environment can affect an organism. Either it can directly affect the physiological processes of the organism or it can impinge upon a sensory receptor of the organism to cause a response.

Let us consider first the nature of the physiological interaction with the environment. The marine environment exhibits variation with time and space.

In order for an organism to inhabit a particular space in this continuum, it must be able to compensate for some degree of environmental variation. Organisms in general exhibit three types of capacities

for dealing with this variation: tolerance, acclimatization, and adaptation. The genetic makeup determines the range of variation which an organism can tolerate. Acclimitization, a product of the previous history of the organism, allows the organism to modify its tolerance to changing factors of the environment, whereas adaptation refers to the ability of a species to adjust to a new range of tolerance by altering its genetic endowment over generations.

For an organism to inhabit a particular habitat, it must be able to tolerate the range of parameters within that habitat. If the conditions change drastically seasonally, it must have the ability to acclimatize to the new conditions. Adaptation would have the effect on a species of allowing it to extend its range of distribution into the extreme limits of its tolerance. At any one point in time, the success of an organism is dependent upon the sum total of these three dynamic capacities.

Let us now consider the possible consequences of the interaction of the environment. Three major consequences are resultant. If the animal is unable to tolerate one or more parameters of the environment either in space or in a time-space relationship, the animal dies, affecting the rate of mortality of the population, and hence, the distribution and abundance of the species population. If the organism is able to tolerate all environmental parameters so that all biological activities operate at an optimal level, the probability of success of the organism within this habitat is high, producing a high density or abundance.

Between these two extremes, a range of results can occur. If the animal is able to tolerate the parameters of the environment, yet is unable to perform its biological activities at an optimal level, an indeterminate range of probabilities of success of the species within this habitat results. To illustrate this point more clearly, let us consider some of the sublethal effects. If the physiological processes of the organism are operating at a suboptimal level, its feeding rate may decrease reducing its energy reserves and thus decreasing the energy available to carry out its biological activities, making it less able to compete with competitors, less able to escape predators, and so on. Population density would be much lower in this area either from decreased survival probability and/or decreased reproductive potential, hence affecting the regulatory mechanisms of its population dynamics. We will return to some of the sublethal effects later in considering specific pathways through our model.

The alternate pathway in which the environment has a direct effect on the organism is through the ability of the animal to sense changes in the environment. In order to increase the survival potential of a species, each species has evolved a distinct set of behavioural adaptations. If an organism is able to sense a particular parameter, it may have evolved a behavioural mechanism related to variation in this parameter increasing the ability of the species to survive in a particular habitat. The ability of the organism to sense a particular parameter allows it to interact with the environment before an effect on the physiological process is registered. Such behavioural mechanisms can lead to habitat selection, food niche selection,

predator-prey interactions, and a wide variety of other external manifestations of behaviour.

Specific Pathways

From the hypothetical model, we can draw a number of specific pathways that link the individual environmental parameters through the intervening variables to the dependent variable, the distribution and abundance of a species. Since the causal pathways vary with species, not only in the specific directions and linkages, but also in the causal effect of each linkage, we can utilize this model to demonstrate how (and why) different sea star species exhibit different abundance-distribution patterns within a specific range of environmental parameters. Since many parameters have similar variation patterns in terms of their spatial distributions, we can determine which factors are actually operating to affect distribution and abundance by demonstrating valid causal linkages between the individual environmental parameters and the dependent variable. Those parameters which cannot be shown to demonstrate valid linkages with the intervening variables can be excluded as being unimportant in affecting distribution and abundance of the particular species within a specific habitat. The approach is therefore to consider each parameter of the environment individually, and to trace the pathways established by this present study and by previous studies differentiating by species.

I. Depth

Evidence for Relationship between Depth and Abundance-Distribution Patterns

All species demonstrated some correlation between their abundance-distribution pattern and depth. L.polaris and A.vulgaris both had

negative correlations, whereas H.eschrichti demonstrated a positive correlation. Both C.papposus and S.endeca were found only below a depth of 18 meters.

Possible Intermediate Pathways

Although depth is commonly used in defining the space occupied by a species of sea star, little evidence exists to justify this parameter as a regulator of abundance and distribution. Since many parameters demonstrate a relationship with depth, it is more likely that one or more of these depth-dependent parameters is responsible for regulating abundance and distribution of a species. The most direct proof of this hypothesis is that many species demonstrate different bathymetric distributions over the extent of their geographic range. A.vulgaris can be used as an example. In the northern part of its range (Newfoundland-Labrador), this species is found in shallow water, whereas in the southern limits of its range, it is exclusively found in deep water (Galtsoff and Loosanoff, 1939; Gray et al, 1968).

Let us consider the model briefly to determine why depth would be unimportant as a distribution regulating mechanism. The only depth-dependent environmental parameter that has a relatively fixed relationship with depth is pressure. Since sea stars have a hydrostatic skeleton, it would appear that they would have a large tolerance for pressure changes. Hence, pressure changes within relatively wide limits would have little effect on the probability of survival of a species.

The ability of sea stars to detect pressure changes has not been established. The probability, however, of their possessing a pressure

receptor would seem to be high, since they have a hydrostatic skeleton which must be adjusted for pressure changes. Since the physiology and biological activities of sea stars would appear not to be affected by small pressure changes, it is difficult to speculate on a behavioural adaptation that would have evolved as a direct result of having a pressure receptor.[1]

Summary

Although depth is important in describing the geographic distribution of a species, it would appear to be unimportant in regulating distribution and abundance of the studied sea star species within a small range of depth as exhibited in the study area. Distribution and abundance of the studied species would appear to be controlled by other environmental parameters which may vary with depth at a specific location. Since the pressure tolerance of the studied species would seem to be wide, pressure can be excluded from this list of depth-dependent parameters affecting the distributions and abundances of sea stars inhabiting the study area.

II. Slope

Evidence for Relationship between Slope and Abundance-Distribution Patterns

The abundance-distribution pattern of H.eschrichti demonstrated a strong positive correlation with steeply sloped areas. Density of individuals was higher on steeply sloped areas than on less sloped

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[1] Indirectly, a behavioural adaptation to pressure changes may have evolved if a depth-dependent environmental parameter that sea stars are incapable of sensing, has an effect on the physiology or the biological activities of a sea star. The likelihood of this occurring is small because the vertical distribution of environmental parameters is not constant over the geographic ranges of the studied species.

areas. L.polaris and A.vulgaris exhibited this relationship to a lesser degree in their abundance-distribution patterns. No apparent relationship was noted for C.papposus and S.endeca.

Possible Intermediate Pathways

The effect of slope on the distribution of sublittoral populations of sea stars has been largely ignored by previous researchers.[1] The only report of distribution with respect to slope was by Huntsman (1918) who stated that A.vulgaris was absent on a sloped area because of fluctuating temperature.

As was the case for depth, we must face the problem of trying to determine whether the actual physical slope has an effect on the intervening variables, or whether some environmental parameter associated with slope changes affects the intervening variables. Other environmental variables demonstrating a relationship with the sloped areas of the cliff were water disturbance, prey, predators, competitors, and associations. Superficially, it appears that slope has a direct effect on the abundance-distribution of H.eschrichti; however, if we attempt to correlate the abundance-distribution of H.eschrichti directly to tan θ (ie. the slope of each TLQ), we find that no direct relationship actually exists. This relationship appears to be associated, then, with other parameters which are affected by the topographic changes in slope.[2]

Let us examine the possible pathways to determine if this conclusion

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[1] Until the advent of SCUBA gear, sublittoral populations of sea stars on sloped rocky bottoms could not be sampled.

[2] This argument will be dealt with more fully under pathway IV. Water Disturbance.

is valid. It would appear that the angle at which a sea star is oriented to the horizontal plane would have little or no effect on its physiology. Evidence, however, exists that the pull of the body on the podia acts as a gravity receptor (reviewed by Hyman, 1955). Since sea stars have the capacity to sense slope changes, the possibility of a behavioural adaptation to slope changes exists.

The direct effect of slope on biological activities of an animal is also suggested by aspects of this study. In section E-II.3(i,a), we noted that the percentage of L.polaris feeding was lower on areas of steep slope than on the more gentle slopes. Since decreased feeding rate of a species may have an effect on the mortality rate of that species, we would expect a behavioural adaptation to avoid areas of steeper slope. The opposite, in effect, occurred. An abnormally high abundance of L.polaris was observed in TLQ 8, a sampling quadrat on the steeply sloped area. Hence, we see that L.polaris probably has not evolved a behavioural adaptation as a result of an ability to sense slope changes that would allow a greater probability of survival.

Other species apparently have evolved a behavioural response to slope. Asterina gibbosa,(Forbes) according to Crozier (1935) will ascend the perpendicular walls of a glass jar and will repeat the performance if the jar is inverted. It is difficult to interpret this observation in terms of how this behaviour would affect the distribution and abundance patterns of a species. More detailed experimentation must be completed to determine the exact nature of this response before its implications in the process of habitat selection can be understood.

Summary

No direct evidence that sea stars selected their habitat on the basis of a particular angle (or a range of angles) of inclination was indicated by this study. Rather, some species, particularly H.eschrichti demonstrated a relationship with the overall topography indicating that their abundance-distribution pattern was more likely related to another environmental parameter which was affected by the topographic features. A comprehensive study of the behaviour associated with the angle of the substrate is necessary before any implication with habitat selection by the study area sea stars can be justified.

III. Light

Evidence for Relationship between Light and Abundance-Distribution Patterns

Since light and abundance-distribution patterns of the studied sea stars are both related to depth, a possible interrelationship between light and abundance-distribution may exist. Light was found to decrease exponentially with increasing depth. Although the distribution-abundance patterns of L.polaris and A.vulgaris have a linear relationship with depth on the cliff, an approximately exponential pattern with depth exists if we include the values for the MAL zone with those of the cliff. Because of the relationship of H.eschrichti to steeply sloped areas, it is impossible to relate the abundance-distribution pattern of this species to an exponential equation. If we assume that S.endeca and C.papposus avoid areas of high light intensity, a possible relationship between light and distribution and abundance may exist.

Possible Intermediate Pathways

Although Hyman (1955) states that light appears to play a considerable role in the life of asteroids, little work, apart from

studies of phototaxis, has been done to support this claim. Sea stars may respond actively or passively to light. Numerous studies have demonstrated that sea stars possess an ability to sense light by means of either a generalized dermal light sense and/or by a specialized photoreceptor (called the optic cushion) located on the terminal tentacle at the tip of each ray (Yoshida, 1966). It is probably safe to assume that light does not have a direct effect on the physiological processes without first impinging on the photoreceptors of the organism. Indirect physiological responses due to the ability of sea stars to detect light have not yet been studied. Hence, the pathway that is most valid is that light affects the photoreceptors which in turn may affect either the physiology or the behaviour of the organism.

Physiological or behavioural responses[1] can be examined by their effect on the biological activities of the species. Sea stars as a group, elicit a variety of phototactic responses to light.[2] In the present study, we also found that a considerable variation in responses existed between species. These species differences may account for differences in their abundance-distribution patterns, but difficulty arises in determining the exact relationship between light, light response, directed movements, and distribution and abundance. The difficulty occurs if we assume that sea stars displaying a strong phototactic response, tend to move progressively towards shallow

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[1] It must be acknowledged here that behavioural responses are more likely the dominant factor affecting the biological activities. Since nothing is known about the passive physiological responses to light, the physiological pathway is also included as a possible response to light variation.

[2] Part of this reported variance is due to uncontrolled experimental methods.

water where light intensity is the strongest. Coincidentally, the four studied sea star species demonstrated this relationship. L.polaris and A.vulgaris which had the strongest phototactic response are highest in abundance in shallow water, whereas C.papposus and S.endeca displayed a weaker response and were found in deeper water. This hypothesis, however, must be rejected because A.vulgaris is found in shallow water in northern waters, but is found in deeper water in the southern part of its geographic range.

A more plausible explanation results if we consider a series of experiments by Castilla (1971). He demonstrated that A.rubens could be adapted to light conditions different from its habitat so that the actual phototactic response could be reversed. The implications of these results are that sea stars found in a particular habitat have adapted to that light regime and are not found in a specific habitat because of a constant light behaviour which causes them to select a habitat with specific light properties.

Obviously this hypothesis is simply an extrapolation from the results of a series of experiments on one species. It may be invalid to generalize the behaviour of A.rubens for all sea stars, but the many contradictions in the literature (Hyman, 1955) concerning the phototactic responses of a particular species, suggest that light adaptation is a fairly widespread phenomenon. Hence, the pathway:

light → sensory reception → behaviour → migration and movement
→ distribution and abundance i.e. habitat selection

based on an optimal light regime, probably does not function to any

significant extent to influence large scale movements of populations.

Although it has been shown that the feeding rate of some species, eg. Astropecten irregularis (Christensen, 1970); Astropecten polyacanthus (Muller & Troschel) (Mori and Matutani, 1952), is affected by the daily light rhythms, all study area species, with the exception of Henricia species were observed[1] also feeding at night. Some effect of variation in daily and seasonal changes in the properties of light may affect differentially the feeding rates of the studied species to cause the unique distribution and abundance patterns associated with each species, but this is unlikely.

Light may have an effect on the reproductive cycle of sea stars, but this area has not been researched.

Summary

Since sea stars have the capacity to adapt to specific light conditions within a short period of time, it is very unlikely that sea stars select a habitat on the basis of small changes in light over short depth range as experienced in the study area. Although the physiological processes of sea stars may be affected differently by light, insufficient research has been completed to demonstrate the ultimate effect of this pathway on the distribution and abundance of a species. The biological activities of sea stars vary, but the differential effects of light on the various species have not been established to the extent that light can be demonstrated to be a controlling factor of habitat differentiation.

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[1] The feeding biology of H.eschrichti and Henricia sp. was not studied because of the difficulty in determining when these suspension feeders were actually feeding.

IV. Water Disturbance

Evidence for Relationship between Water Disturbance and Abundance-Distribution Patterns

In this study, sea star species demonstrated a variance in their capacity to attach themselves to the substrate (refer to Pull Capacity Experiments, section H). Since both water disturbance, and distribution and abundances were determined to vary with depth and topographic features associated with slope gradients, a possible interrelationship between the ability of sea stars to resist water disturbance, distribution of water disturbance, and the abundance-distribution patterns of a species may exist.

Species which had their peak abundances in shallow water, L.polaris and A.vulgaris, demonstrated a greater pull capacity than those species whose abundances were highest in deeper water, H.eschrichti, C.papposus and S.endeca. Since water disturbance decreases with depth, a direct relationship between the amount of water disturbance, the ability of the sea star species to resist water disturbance, and their abundance-distribution patterns, exists and therefore water disturbance appears to be a strong factor controlling distribution. Of those species found in shallow water, a preference for protected areas was demonstrated. Some species differentiation was noted here. L.polaris, a species which demonstrated an extremely high pull capacity was found to inhabit more exposed areas in the MAL zone than A.vulgaris, a species which had a comparatively lower pull capacity.

Steeply sloped areas, which were found to have a lesser degree of water disturbance than the more gently sloped areas, were preferred

by H.eschrichti, a species with an extremely low pull capacity. C.papposus and S.endeca were found to be excluded from areas of high water disturbance.

Possible Intermediate Pathways

The pathway suggested by this relationship is that water disturbance acting through the capacity of a sea star to resist it, results in species differentiation in distribution and abundance. Several possible pathways exist connecting these three variables.

First, let us consider the direct effects of water disturbance on sea stars. If the force of water disturbance exceeds the capacity of a sea star to resist it, the sea star will become disattached from the substrate and translocated to another location. This translocation process would take place until the sea star is shifted into a location in which it is able to resist the disturbance. All sea stars which are capable of resisting this force would remain in their present position. In this way, patterns of abundance-distribution of each species would exactly resemble their capacity to resist water disturbance directly following a period of a high degree of water disturbance.

Although this may be a plausible hypothesis, it is impossible to support by means of field observations. Obviously, conditions in which sea stars would be dislodged from the substrate do not permit diving. Hence, this phenomenon cannot be observed.[1]

To avoid this type of translocation, it would be advantageous for

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[1] This hypothesis however, can be tested in the laboratory. If a number of sea stars are placed in a tank and water allowed to flow at high pressure, sea stars forced off the bottom of the tank will be translocated to a position of low turbulence.

sea stars to have evolved behavioural adaptations to select habitats with a level of water disturbance within their range of resistance. Since sea stars are capable of sensing currents (positive rheotaxis, eg. demonstrated in A.rubens, (Castilla & Crisp, 1970)), they may be able to sense areas of high and low turbulence, and hence, would move until they found a less exposed area. This is a difficult hypothesis for which to provide support because the amount of water disturbance is not constant within the environment. Consider sea stars situated in the MAL zone. During periods of calm, sea stars would have no means of sensing areas which are less exposed and would move out of locations of protection (i.e. areas that would be protected during a period of a high water disturbance) in search of food. With the onset of turbulent conditions, sea stars would then have to seek out areas of protection. This would involve a movement under stress conditions with no means of orientation to areas of protection. In other words, it would be a trial and error approach. The sea star would cease activity only when an area of suitable protection was encountered. This behavioural mechanism would involve rheokinesis, i.e. increased activity in conditions of water movement and decreased activity during conditions of no water movement. No studies of this type have been undertaken to elucidate the possibility of this hypothesis.

The degree of water disturbance may have an effect directly on biological activities. The effect of water disturbance on feeding and reproduction should be examined to determine whether an interspecific variance in these effects would differentially affect sea star species

abundance-distribution patterns.

Physiological processes may be affected by the alteration of biological activities due to the effect of water disturbance, but a direct effect on the physiology of a sea star apart from physical damage encountered during periods of high water disturbance, appears unlikely.

Summary

The question of whether sea stars respond actively to water disturbance by selecting habitats with protection, or whether sea stars are passive subjects being translocated by water movement, is an unanswered one based on research hitherto undertaken. It appears conclusive, however, that one or both of these pathways is responsible for causing such a high correlation between distribution of water disturbance and abundance-distribution patterns of each species. Habitat diversity of the sea star species within the study area appears to be controlled by the interrelationship of the ability of a species to resist water disturbance and the distribution of water disturbance.

V. Temperature, Salinity (Conductivity), and Dissolved Oxygen Concentration Evidence for the Relationship Between Temperature, Salinity, and Dissolved Oxygen Concentration and Abundance-Distribution Patterns.

Except for a short period of the year, June to September, vertical stratification of these environmental parameters does not exist within the study area. Unless we assume that this gradient affects the abundance-distribution patterns during this critical period, no direct correlation exists.

Possible Intermediate Pathways

Owing to the complexity of interrelationships involved between these environmental parameters, the physiological and biological activities, population dynamics, and abundance-distribution of a species, these pathways must be broken down into their individual components to determine whether the distribution and abundance of a species may be ultimately affected by the particular temperature, salinity, and dissolved oxygen concentration regime(spatial and temporal)characteristic of the study area. The following intermediate pathways must be considered:

(a) Habitat Selection

T,S,(O) → sensory reception → behaviour → motility → migration → distribution and abundance

(b) Tolerance

T,S, (O) → physiology → mortality → distribution and abundance

(c) Sublethal Physiological Effects

T,S, (O) → Biological activities → population dynamics → distribution & abundance
→ physiology ↗

(a) Habitat Selection

Little work has been performed towards determining whether sea stars are capable of detecting differences in temperature, salinity, and dissolved oxygen concentration, and thereby capable of selecting levels which allow optimal probability of success. One of the few studies in this area was performed by Polunina (1965), who demonstrated that A.rubens will select water having a salinity of 34 parts per

thousand over water having a salinity of 23 parts per thousand, but will not differentiate between waters with salinities of 24 parts per thousand and 34 parts per thousand. Therefore, in an environment where usually small salinity gradients exist, such as the study area, A.rubens would not select a habitat on the basis of salinity. Species differences may exist in this regard depending on the ability of a species to tolerate salinity changes. A.rubens which has a high tolerance of salinity may be relatively insensitive to salinity changes, whereas a stenohaline species may be very sensitive to salinity gradients.

Similarly, work on selectivity of habitat based on the ability of sea stars to detect temperature and dissolved oxygen concentration gradients is non-existent.

We cannot entirely exclude the possibility of some degree of habitat selection because of lack of experimental studies in this area. However, habitat selectivity would appear unlikely because of the relatively short-lived and fluctuating nature of the gradients characteristic of these parameters in the study area.

(b) Tolerance

For each species of sea star, the zone of tolerance of these parameters can be clearly delineated in terms of an upper and lower tolerance level. If the value of one of these parameters or the combined values of more than one parameter fall outside of this range, death of the sea star occurs, thus limiting the distribution of a species to the spatial and temporal range of these parameters, which fall within the zone of tolerance of the species.

Since H.eschrichti, A.vulgaris and L.polaris are found in all areas of the study area, tolerance of these parameters would appear not to be a factor limiting their distribution in the study area. A similar argument cannot be employed, however, for C.papposus and S.endeca. Since these two species are limited to the deeper section of the study area, perhaps the parameter gradient during the critical period (June - September) operated in a time-tolerance relationship to limit C.papposus and S.endeca to deeper water. Some support for this hypothesis is provided by Ursin (1960) who stated that S.endeca "avoids" (sic) areas with a mean temperature of more than 14°C in the warmest month, also requiring a salinity of at least 30 parts per thousand. This hypothesis can be rejected, however, based on laboratory observations. Representatives of both these species were maintained successfully in the laboratory during the critical period under ambient shallow sea water supply.

(c) Sublethal Physiological Effects

Within the range of tolerance of an organism, many of its biological activities are affected differentially at different values of these parameters. Most of the literature in this regard has been devoted to studies of the effects of temperature on various biological activities. Temperature has been shown to affect feeding rate (Hancock, 1958; Mackenzie, 1969; Galtsoff and Loosanoff, 1939; Smith, 1940); rate of locomotion and righting (reviewed by Hyman, 1955); and reproductive cycle (Feder and Christensen, 1966).

The efficiency with which each species can carry out its biological activities, then, is dependent upon its capacities of

acclimatization, adaptation, and tolerance. Dependent on the efficiency with which a species can carry out its biological activities, is the success of that organism in its particular habitat. If the species cannot carry out its biological activities to an optimum, the negative effect of exogenous factors[1] on its population dynamics is magnified. On the other hand, if an organism is well adapted to the temperature, salinity, and dissolved oxygen concentration regime and can carry out its biological activities at an optimal level, the pressure exerted by negative exogenous factors of the environment is lessened.

Summary

Habitat selection and tolerance with respect to temperature, salinity, and dissolved oxygen concentration are assumed to have an insignificant effect on the distribution of sea stars in the study area because of the short-lived and fluctuating nature of these parameter gradients. However, differences in the sublethal physiological effects of these parameters upon the biological activities affect the ability of each species to cope with negative exogenous factors within the environment.

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[1] The term 'negative effect of exogenous factors' is employed here to represent the host of factors that exist within an environment that an organism must resist in order to survive. Such factors would include predation pressure, prey resistance (abundance, availability, and defense mechanisms of prey, etc), and competition from other organisms whose niche overlaps that of the studied species.

Biological Environmental Parameters

I. Prey

Evidence for Relationship Between Prey and Abundance-Distribution Patterns

The area of greatest abundance of L.polaris and A.vulgaris overlaps with the area of greatest abundance of their primarily preferred prey, M.edulis. In this area, the MAL zone, distributions of A.vulgaris and L.polaris had a positive correlation with mussel distribution during the summer period.

H.eschrichti, a suspension feeder, has its greatest abundance in areas where suspended material is most likely to fall.

A considerable body of literature exists on the ability of sea stars to detect prey and move towards it. This ability appears to be related to a chemoreception associated with the tube feet.[1] Feder and Christensen (1966), in reviewing this phenomenon, state that "sea stars generally do possess the ability to sense food at a distance, although definite evidence is lacking for the Solasteridae." However, evidence presented in this study showed that S.endeca pursued a prey species six meters away by moving onto a substrate (sand) not usually inhabitated by individuals of this species in the study area. Feder and Christensen (1966) conclude by stating that movement in the field is probably not

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[1] A variety of opinions have been expressed regarding the location of the chemoreceptors responsible for this behaviour. Feder and Christensen (1966) and Hyman (1955) cite four studies which comment on the location of these receptors: on the underside of each arm (Romanes, 1883); in tube feet at the tips of the arm (Prouho, 1890); on the surface of the tube feet, mainly on the podia near the end of each arm (Regnart, 1928); and on all tube feet, but mainly on modified tube feet at the tips of each arm which are entirely sensory (MacGinitie and MacGinitie, 1949).

controlled by food except over short distances dependent upon species, current conditions, intensity and concentration of perceptible matter.

In an earlier discussion, it was hypothesized from the data how the aspects of food generalism and prey selectivity affect the distribution patterns of the study area species. It was speculated that prey generalism allowed A.vulgaris and L.polaris to inhabit any areas that had at least one prey species, whereas prey selectivity tended to concentrate these predators in areas of their primarily preferred prey. For C.papposus and S.endeca, it was speculated that combined predation pressure by both species could reduce the numbers of their primarily preferred prey, but that their practice of prey generalism allowed them to remain in a specific habitat feeding on other prey items until their primarily preferred prey immigrated into or settled in that area.

Although prey probably does not directly affect the physiology of a sea star, lack of feeding due to low prey abundance can affect the physiology of the sea star, and hence affect other biological activities and population dynamics regulating the abundance-distribution of a species. Since behavioural adaptations appear to have taken place in A.vulgaris and L.polaris that result in their being absent from areas with low prey abundance, habitat selection appears to be the major pathway correlating predator and prey abundance-distribution patterns.

It is difficult to comment on the high abundance of H.eschrichti in areas of high settlement of particulate matter. This correlation is also coincident with areas of low water disturbance, discussed earlier as being important in regulating the distribution and abundance of this species. Since both of these conditions, i.e. low water disturbance and high food concentration appear to be essential to the

survival of this species, H.eschrichti appears to be well adapted to this natural correlationship of these parameters in the environment.

Summary

Correlation between prey abundance and sea star abundance appears to be controlled by a large number of intervening variables such as ability to perceive prey, behavioural feeding adaptations, prey selectivity and food generalism, and prey characteristics. The distribution and abundances of A.vulgaris and L.polaris appear to be affected by the abundance of their primarily preferred prey; whereas the distribution and abundance of C.papposus and S.endeca cannot be directly correlated. H.eschrichti appears to be concentrated in areas of high food abundance, but the mechanism by which this occurs cannot be hypothesized until further experimental research is performed on this topic.

II. Predators and Competitors[1]

Evidence for Relationship Between Predators and Competitors and Abundance-Distribution Patterns.

In section I, the direct evidence for this pathway was discussed and the following conclusions were made:

1. Behavioural interactions between species and between members of the same species were demonstrated to be related to competition and predation.

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[1]Since sea stars are both the major competitors and predators of sea stars as a group, both of these parameters are considered together.

2. On the macroscale distribution, ie. within the study area, competitors were found to have similar distribution patterns, and the area of greatest abundance of A.vulgaris and L.polaris was found to be in an area which was not inhabited by their major predators, C.papposus and S.endeca.
3. The major impact of these two dimensions, i.e. competition and predation, was most evident in aggregation formations, ie. in the microdistribution within the study area.

Possible Intermediate Pathways

Principally, there are two known pathways by which predators can affect the distribution patterns of their prey:

(i) Firstly, by feeding on its prey, the predator directly affects the mortality rate of the prey species, and hence affects the abundance-distribution patterns of the prey species.

(ii) The second route, ie. habitat selection, is based on the ability of the prey to perceive its predator before capture. The causal pathway then would be:

predators → sensory reception → behaviour → movement → migration → distribution and abundance

Competitors may affect distributions and abundances of sea star species also by means of two distinct pathways. The first effect results directly from competition for the same food resource. If the food source is limited, the species which is best adapted to a particular habitat will have the greatest advantage in vying for this food resource. Competitive pressure may have the effect of reducing

the feeding rate of one or more species hence affecting their physiology. Decreased physiological efficiency would have a rebound effect on other biological activities such as reproductive potential, and motility and attachment. Considered to an extreme, certain aspects of the population dynamics of one or more competitors would be affected, thus affecting distribution and abundance. Note also that decreased physiological efficiency due to competition may exaggerate the effect of other negative exogenous parameters of the environment on the population dynamics of a species.

The second pathway, dealt with in some detail in section I, results from the ability of sea stars to perceive other sea stars by means of chemoreception. Dependent upon the degree of competition between species, limitations in food resources (or space, if spatial competition is involved), a variety of behavioural adaptations may evolve which affect the abundance-distribution patterns of the competitors.

Toxic properties of sea stars represent a third possibility in which competitive and predatory sea stars may affect the distribution and abundance of a particular sea star species. It has been demonstrated by several authors that sea stars have toxins which prove fatal to specific organisms (Madsen, 1955; Hoshimoto and Yasumoto, 1960; Yasumoto et al, 1964). Chaet (1962) demonstrated that toxins, derived from the coelomic fluid of scalded Asterias forbesi, injected into healthy specimens of A.forbesi and other selected sea star species, caused autotomy and death. However, experimental evidence (gathered

either in the laboratory or the field), that a sea star is directly affected physiologically by the presence of another sea star is lacking.

These pathways, ie. those involving predator-prey and competition relationships, can best be assessed from the relative abundances of each species within the study area.

Consider first the relative abundances of competing species. In the MAL zone, A.vulgaris was dominant in numbers over its competitor, L.polaris. It was also discovered that A.vulgaris had a greater tendency to position itself with respect to food, M.edulis, and to areas of protection than did L.polaris. In the laboratory, it was shown that L.polaris occasionally exhibited an avoidance response to A.vulgaris while at rest and while feeding. If we assume that L.polaris was forced out of these favourable areas by this interspecific behaviour, it is clearly demonstrated that A.vulgaris would have a higher probability of success in this area.

In the cliff area, however, L.polaris proved to be dominant in numbers over A.vulgaris. As far as A.vulgaris is concerned, food may be a limiting factor in this area. As noted in the feeding studies, A.vulgaris had a higher dependency on M.edulis than did L.polaris in the study area, and demonstrated a higher rate of feeding than did L.polaris in laboratory experiments. In the cliff area, L.polaris fed to a greater extent than A.vulgaris on molluscs, whereas A.vulgaris fed on abundant echinoderms such as sea urchins and brittle stars. If we assume that A.vulgaris requires a higher rate of feeding than L.polaris to survive

in this environment, its practice of feeding on the most available food resource, echinoderms, rather than on the food source which is higher in caloric value, molluscs[1], as does L.polaris, it appears to be at a competitive disadvantage in the cliff area.

Regarding the remaining two competitive species pairs, i.e. H.eschrichti and Henricia sp., and S.endeca and C.papposus, competition is more difficult to assess. In these cases, one species of each pair is much more dominant numerically and this dominance appears to involve reproduction in addition to competition. Since the dominant species in each competitive pair (H.eschrichti and C.papposus) is well established, the opportunity for invasion of these niches by the non-dominants is severely affected.

Superficially, it appeared that C.papposus was better adapted to its feeding niche than was S.endeca. C.papposus demonstrated a high degree of voracity, feeding on a wide variety of abundant prey items, whereas S.endeca fed at a low feeding rate on a very restricted diet, specifically on Cucumaria frondosa. Competition between S.endeca and C.papposus for food resources may have restricted the diet of S.endeca to a low abundance prey item, C.frondosa, hence reducing its probability of survival in this particular habitat. Evidence of inter-specific behaviour also tended to suggest a slight advantage to C.papposus. Resting S.endeca exhibited an escape response to C.papposus but resting

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[1] Reddin (1973) in calculating the average number of calories per gram dry weight (excluding calcareous parts) lists values of 4448 and 3448 for M.edulis and S.droebachiensis respectively.

C.papposus demonstrated only an avoidance response. During feeding, however, neither species was forced from its prey by contact with its competitor.

The competitive advantage of H.eschrichti over Henricia sp. is unclear based on differences with respect to behavioural interactions and feeding niches. Since the feeding biology of these two species of suspension feeders was not studied, feeding differences could not be assessed. The only differences noted during this study were that Henricia sp. appeared to have a slightly shallower distribution, preferring a sponge substrate, rather than the tunicate substrate preferred by H.eschrichti. Breeding difficulties may account for the low abundance of H.eschrichti.[1]

Although C.papposus, the major predator of H.eschrichti, L.polaris and A.vulgaris, obviously has an effect of reducing their abundances, good correlation between the R.A. values of C.papposus and the R.A. values of its prey does not exist. Throughout TLQ's 6-18, the R.A. values of L.polaris and A.vulgaris remain roughly constant, whereas the R.A. values of C.papposus peak in TLQ's 11-18. Similarly, the R.A. values of H.eschrichti peak in TLQ's 19-23, an area where C.papposus is found.

In terms of affecting aggregation formation, predators and their prey were never observed in close association except during predation.

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[1] This is a difficult area to assess because it has been speculated (Grainger, 1966; Rasmussen, 1965), that there is the possibility of interbreeding between Henricia spp. Since these species present difficulties to the taxonomist (Grainger, 1966), perhaps the question of competition should be omitted.

Summary

Competition tended to have an overall effect on the distribution patterns of the species found within the study area, but predation did not clearly demonstrate a relationship with distribution and abundance patterns that could be linked solely to the distribution of predators. Microdistribution, ie. aggregation formation, can be directly linked to the combined effects of predation and competition.

III. Associations

Evidence of the Relationship Between Association and Abundance-Distribution Patterns

Only one example of other groups being associated with sea stars was found to exist in the study area. As previously discussed, this relationship between two suspension feeders, members of the genus Henricia, and a tunicate, Didemnum albidum, was termed 'energy commensalism' by Rasmussen (1965). General observations indicated that Henricia was often found on or very near this tunicate. If we examine the distribution patterns of these two species (Table 3 for D.albidum and fig. 21 for H.eschrichti) we see that the major peak in abundance of H.eschrichti overlaps with the distribution of D.albidum, ie. in TLQ's 19-24. As far as individual samples are concerned, both species had their highest abundance in TLQ 22.

Possible Intermediate Pathways

The pathway that is assumed to exist here is habitat selection based on the ability of sea stars to perceive currents (rheoreception), or to perceive matter released by the tunicate (chemoreception). In

the laboratory, it was observed that Henricia was attracted to sponge, another current-producing substrate, within a short period of time; hence, a similar behaviour is probably exhibited by H.eschrichti in the field with respect to D.albidum. One can only speculate, however, on the distance over which this behavioural mechanism operates.

Difficulty exists, however, in demonstrating the degree to which this factor is responsible for concentrating H.eschrichti. Since the areas of concentration are characterized by less water disturbance and by a high rate of settlement of food material, factors which in previously discussed sections have been hypothesized to concentrate the distribution of H.eschrichti, the Henricia-tunicate association appears to be only one of the factors which is important in governing its abundance-distribution patterns. Since this association is not necessary for Henricia to survive (i.e. note the high concentrations of H.eschrichti in area B), it can be assumed that this factor is not as important as water disturbance in regulating the abundance-distribution of this species.

Summary

Although a direct effect of this parameter has been demonstrated by means of an intermediate pathway, its role does not appear as significant as water disturbance in regulating the distribution and abundance of Henricia.

General Summary and Concluding Remarks

The local distribution and abundance of a species can be controlled by a wide range of interactions between members of that species and their environment. Some interactions evidently have stronger influences on abundance-distribution patterns than others, and in this study, results of interactions were shown to directly lead to differences in patterns of distribution between asteroid species.

Biological activities of asteroids, such as feeding behaviour, reproductive biology, motility, and attachment to substrate, demonstrate the effects of these interactions, and the distribution and abundances demonstrate the degree of success each species has enjoyed in these interactions.

By way of summary of these interactions, we can list the following conclusions:

1. Depth, slope, and light per se had little or no visible overall effect on the distribution of these species; however, other parameters associated with these parameter gradients may have had direct influences.

2. Temperature, salinity, and dissolved oxygen concentration gradients probably did not directly affect the distribution of sea stars within the study area; but the degree with which the combination of these factors affect their biological efficiency may affect the ability of the species to cope with negative exogenous factors in their environment, thus affecting their distribution and abundance patterns.

3. Distribution of water disturbance, prey, predators, and competitors appeared to be the major factors[1] affecting the abundance-distribution patterns of the asteroid species in the study area. Species varied in their interactions with these parameters to produce the unique abundance-distribution patterns of each species. A summary of the environmental factors affecting these patterns of each species follows.

Asterias vulgaris

A.vulgaris was not limited to a great extent by water disturbance; however, it was associated with protected areas during periods of high water disturbance. Prey appeared to be the major factor concentrating its distribution in the MAL zone. In the cliff area, its distribution was limited by low abundance of suitable prey resulting from competitive pressure by L.polaris, and by a low abundance of its primarily preferred prey, M.edulis. Predation by C.papposus (and possibly by S.endeca), may have had some effect on reducing its abundance at depths greater than 18 meters.

Leptasterias polaris

Water disturbance appeared to have a lesser effect on this species than it did on A.vulgaris because its association with protected areas during periods of high water disturbance was not as noticeable. The abundance of L.polaris in the MAL zone appeared to be limited by competition with A.vulgaris; however, its superior competitive ability

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[1] The association of Henricia spp. with the tunicate, D.albidum, may also have had a slight effect on their distribution.

on the cliff area produced high abundances in the upper three-quarters of this area. Predators reduced its abundance below 18 meters.

Henricia eschrichti

Water disturbance appeared to be the major environmental parameter controlling the distribution of this species, limiting high abundances to areas of low water disturbance. The effect of competition with Henricia sp. was not demonstrated. Predation by C.papposus probably reduced its abundance, but its effects could not be assessed because the abundance of H.eschrichti peaked in the area inhabited by its predator. In addition to low water disturbance, the steep slopes on which this species had its highest abundances, were also characterized by a higher rate of sedimentation, and on the deeper sloped area by the presence of D.albidum, suggesting that the unique combination of these three favourable conditions in areas of steep slope is responsible for high concentrations of this species.

Crossaster papposus

Water disturbance is assumed to be the factor which limits the distribution of this species to deeper water. Prey abundance is lower and competitor abundance is higher in deeper water than shallow. Lack of predators of this species characterizes both areas.

Solaster endeca

The abundance distribution of S.endeca appears to be affected in a similar manner as C.papposus, except that the competitive pressure by C.papposus appears to have contributed to the low abundance of this species.

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Appendix A. Annual (1970-71) temperature (in degrees Centigrade) regime of the study area at six depths.

Appendix B. Annual (1970-71) conductivity (in millimhos/cm) regime of the study area at six depths.

Appendix C. Annual (1970-71) dissolved oxygen concentration (in parts per million) regime of the study area at six depths.

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1 Temperature readings for Feb. 2, Feb. 9, Mar. 2, and Mar. 9, 1971 were $-1.5^{0}C$ at all depths.

APPENDIX A

Depth (m)	Aug. 7	Aug. 14	Aug. 25	Sept. 4	Sept. 14	Oct. 16	Oct. 22	Nov. 10	Nov. 27	Dec. 4	Jan. 14	May 4	May 12	May 19	May 27	June 3	June 9	June 17	June 24	July 1	July 7	July 14	July 21	July 28
10	9.2	13.2	11.1	10.2	10.2	8.1	8.1	6.2	4.8	3.9	0	1.2	1.5	1.8	2.5	5.0	5.8	6.2	7.9	7.5	7.8	8.0	9.0	9.0
15	8.2	13.0	11.0	10.0	9.8	8.2	8.0	6.0	4.7	-	0	1.2	1.5	1.8	2.5	4.8	5.8	5.8	7.2	7.5	7.8	8.0	8.5	8.2
20	3.2	12.9	10.5	10.0	9.5	8.1	8.0	5.9	4.7	-	0	1.2	1.5	1.0	2.2	4.2	5.5	4.0	7.0	7.2	7.2	8.0	8.1	7.8
25	2.1	12.5	10.5	9.8	8.5	8.1	8.0	5.8	4.5	-	0	1.2	1.5	0.8	2.2	3.9	2.0	3.2	6.2	6.0	7.0	8.0	6.1	7.2
30	1.8	9.1	10.5	8.2	7.2	8.0	8.0	5.8	4.4	-	0	1.2	1.2	0.5	2.0	2.9	1.0	1.8	4.0	5.0	6.8	7.8	5.5	6.8
31	1.8	7.5	10.5	7.2	6.0	8.0	6.0	5.8	4.4	-	0	0.2	1.0	0.5	2.0	1.5	1.0	1.5	3.0	5.0	6.5	7.8	4.9	4.2

APPENDIX B

10	32.3	34.4	32.6	32.0	32.0	-	29.4	28.5	28.2	28.5	25.3	26.2	26.9	27.2	26.2	26.7	26.4	27.4	24.3	27.9	26.7	22.3	27.2	24.8
15	31.6	34.4	32.6	32.0	31.6	-	29.7	28.5	28.2	28.5	25.3	26.2	26.9	27.2	26.4	26.4	26.7	26.9	24.6	27.9	26.7	22.8	26.9	23.1
20	27.9	34.4	32.6	32.0	31.3	-	29.7	28.5	28.2	28.5	25.6	26.2	26.9	27.2	26.4	26.2	26.7	26.2	24.6	27.9	26.7	22.8	26.7	23.4
25	27.4	34.0	32.6	32.0	30.9	-	29.7	28.5	28.2	-	25.6	26.2	26.9	26.4	26.4	26.2	24.6	25.3	24.6	26.9	26.7	22.8	25.9	23.1
30	26.9	33.2	32.6	30.6	28.5	-	29.7	28.5	28.2	-	25.9	26.2	26.9	26.4	26.2	25.3	24.0	24.8	22.9	26.7	26.4	22.8	25.3	22.8
31	26.9	31.6	32.3	29.4	29.1	-	28.5	28.5	28.2	-	25.9	25.6	26.9	26.4	26.2	24.3	24.0	24.8	22.9	26.7	26.4	22.8	25.1	21.6

APPENDIX C

10	9.84	8.95	9.38	9.47	9.24	9.53	9.64	9.77	10.32	10.43	11.48	11.93	11.69	11.68	11.29	10.94	10.76	10.52	10.29	10.09	10.13	10.00	10.13	10.11
15	10.16	-	9.34	9.50	9.32	9.55	9.68	9.81	10.31	10.40	-	11.82	11.65	11.84	11.46	10.99	-	10.73	10.27	10.10	10.15	10.07	10.22	10.15
20	11.12	8.90	9.42	9.58	9.36	9.55	-	9.79	10.25	10.49	11.84	11.85	11.51	11.86	11.42	10.99	10.59	11.21	10.24	10.33	10.06	10.12	10.23	10.45
25	11.14	8.94	9.42	9.57	-	9.53	9.82	9.82	10.30	10.47	-	11.83	11.65	11.88	11.32	11.09	-	11.34	10.58	10.43	10.10	10.07	10.40	10.30
30	11.09	10.59	11.07	9.62	9.70	9.53	9.67	9.77	10.17	10.47	11.80	11.79	11.65	11.86	11.45	11.21	-	11.32	10.77	10.44	10.20	10.58	10.85	10.50
31	-	-	-	9.62	9.89	-	9.67	9.77	-	-	-	11.79	11.63	11.94	11.30	-	-	11.36	10.96	10.38	10.27	10.85	10.84	10.41

Appendix D. Measurements of relative irradiance taken on July 20, 1971 at seven depths.

Depth (m)	Relative Irradiance (%)
0	45.0
5	33.6
10	21.9
15	11.8
20	7.9
25	3.7
30	3.0

Appendix E. Number of observed individuals of Leptasterias polaris (≥1.5 cm) per TLQ for 35 sampling dates, including yearly mean number of individuals per square meter of unobscured bottom per TLQ.

TLQ No.	Jul. 30	Aug. 6	Aug. 13	Aug. 24	Sept. 3	Sept. 10	Sept. 15	Sept. 28	Oct. 5	Oct. 15	Oct. 20	Nov. 2	Nov. 9	Nov. 23	Dec. 3	Dec. 17	Jan. 12	Feb. 2	Feb. 9
1	-	-	-	3	4	1	1	3	3	11	7	5	2	9	5	3	-	5	2
2	-	1	2	4	1	3	3	6	5	-	2	1	2	2	4	2	-	3	-
3	2	2	1	5	1	5	4	3	3	7	1	5	4	5	5	1	-	-	-
4	1	-	2	5	2	4	3	6	5	3	2	2	2	6	1	4	-	4	-
5	-	-	-	3	3	2	2	1	2	2	1	2	1	4	2	7	1	-	3
6	-	-	1	-	-	-	1	2	-	1	-	1	-	1	2	1	2	3	1
7	1	1	3	2	1	-	1	2	6	2	2	-	1	2	2	2	1	1	1
8	-	4	5	7	5	2	4	3	5	4	3	1	4	3	4	1	3	1	3
9	-	-	-	2	1	1	3	3	2	3	1	1	3	4	2	2	2	3	1
10	-	-	2	3	1	1	3	-	1	1	-	1	1	1	2	2	1	2	2
11	2	1	1	1	1	2	1	1	5	3	2	-	-	-	2	3	3	-	-
12	2	1	1	1	1	1	2	3	1	3	1	3	-	1	2	1	2	1	2
13	1	1	-	3	2	1	1	1	-	1	2	2	2	1	1	1	-	4	4
14	1	-	-	-	1	1	-	2	2	-	-	6	2	-	-	2	2	3	-
15	-	-	1	-	2	-	-	-	1	-	-	1	1	-	1	3	1	-	2
16	2	1	2	1	-	1	1	1	1	1	1	-	1	2	-	2	-	-	-
17	-	-	1	-	1	1	1	-	1	2	-	2	-	1	1	-	2	1	1
18	-	-	-	1	-	-	-	1	1	1	1	3	1	1	1	-	-	-	1
19	1	2	1	2	-	-	1	-	1	1	1	2	1	-	1	1	1	1	-
20	2	-	4	1	2	-	-	-	-	2	2	-	-	4	-	-	-	3	2
21	1	1	1	-	1	-	-	-	-	-	1	1	1	-	2	3	1	-	1
22	1	1	2	2	1	1	-	-	-	-	-	-	1	1	-	1	1	-	2
23	-	1	2	-	1	-	-	-	-	-	1	1	-	1	-	-	1	-	-
24	-	1	-	-	-	-	1	2	1	-	1	-	-	-	1	-	1	-	-

TLQ No.	Mar. 2	Mar. 9	May 4,6	May 11	May 19	May 26	June 3	June 9	June 17	June 24	July 1	July 7	July 14	July 21	July 28	Total	Square Meters of Unobscured Bottom	No. Individuals/ m^2 Unobscured Bottom
1	1	4	1	-	-	2	2	2	2	1	-	1	1	-	2	83	33.00	2.515
2	2	2	2	1	-	1	1	1	-	1	2	-	1	1	-	56	34.10	1.642
3	-	1	3	-	2	-	-	-	1	3	2	1	1	-	2	70	42.46	1.649
4	-	2	1	1	1	-	1	2	3	-	1	2	2	2	1	71	47.62	1.491
5	1	4	2	3	1	3	1	1	1	2	1	1	2	2	1	62	48.04	1.291
6	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	22	38.24	0.575
7	-	-	-	1	3	-	2	2	3	2	-	-	1	2	1	48	42.04	1.142
8	2	1	2	3	1	3	2	1	4	4	-	2	2	-	-	89	50.86	1.750
9	1	5	1	3	1	1	-	1	1	2	-	1	-	1	1	53	50.95	1.040
10	1	3	-	-	2	-	-	-	2	3	2	-	1	2	2	42	51.00	0.824
11	2	4	4	2	3	-	-	-	-	-	-	1	1	-	-	45	50.96	0.883
12	-	1	1	1	-	-	1	-	-	-	-	-	-	1	4	38	50.88	0.747
13	-	1	1	-	-	1	-	-	-	-	1	-	-	-	-	32	50.97	0.628
14	1	1	1	1	-	-	1	-	1	-	-	-	1	-	4	33	50.88	0.649
15	1	1	-	-	-	1	1	1	-	-	-	-	-	-	-	18	50.97	0.355
16	2	-	-	-	1	1	-	1	2	-	1	-	-	1	1	27	51.00	0.529
17	1	1	-	-	2	3	1	1	2	-	1	1	2	1	1	32	50.96	0.628
18	1	2	1	1	1	-	-	-	1	-	1	1	-	-	2	23	51.00	0.451
19	1	1	-	1	-	-	1	-	-	-	1	1	-	2	-	25	51.00	0.490
20	3	-	1	3	1	-	1	-	1	-	-	3	-	-	-	35	51.00	0.686
21	2	-	-	-	-	-	1	-	-	-	-	-	-	2	-	19	51.00	0.373
22	2	1	1	-	-	1	-	-	-	-	1	-	1	-	-	21	51.00	0.412
23	-	1	-	-	-	-	-	1	-	1	1	4	-	1	1	18	51.00	0.353
24	-	-	3	1	-	-	-	1	-	2	-	-	2	-	1	18	51.00	0.353

Appendix F. Number of observed individuals of Asterias vulgaris (≥1.5 cm) per TLQ for 35 sampling dates, including yearly mean number of individuals per square meter of unobscured bottom per TLQ.

TLQ No.	Jul. 30	Aug. 6	Aug. 13	Aug. 24	Sept. 3	Sept. 10	Sept. 15	Sept. 28	Oct. 5	Oct. 15	Oct. 20	Nov. 2	Nov. 9	Nov. 23	Dec. 3	Dec. 17	Jan. 12	Feb. 2	Feb. 9
1	-	-	-	-	-	-	2	1	-	1	1	-	5	-	4	2	-	1	3
2	-	2	-	-	-	-	1	-	-	1	2	1	-	-	1	3	-	-	-
3	-	1	-	1	-	-	1	1	1	1	5	3	-	-	-	1	-	-	-
4	2	2	-	1	1	2	-	1	2	1	-	-	-	-	-	1	-	-	-
5	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	1	1	1	1	-	1	1	-	-	-	1	1	-	1	1	-	1
7	-	-	-	1	-	1	1	-	3	-	1	1	2	-	2	-	-	-	1
8	1	1	1	1	-	4	7	3	3	1	3	1	4	-	1	2	4	-	1
9	-	-	1	-	-	1	1	-	1	-	2	-	1	1	2	2	1	2	-
10	-	1	1	1	-	-	-	-	1	-	-	1	1	2	4	-	1	1	1
11	-	1	-	-	-	-	-	-	1	1	1	1	-	1	-	-	-	-	-
12	-	-	1	-	-	-	1	-	1	-	-	-	3	1	1	1	1	-	-
13	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	1	-	-	1
14	-	-	-	1	-	-	1	2	1	2	-	3	1	1	-	-	-	-	-
15	-	-	-	-	-	-	-	1	1	1	-	-	-	-	1	1	-	-	-
16	-	1	-	-	2	-	-	-	1	2	1	2	-	-	-	-	-	-	-
17	2	1	2	-	-	-	-	-	1	-	-	2	-	-	1	1	-	-	-
18	2	-	1	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	1
19	-	-	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	2	1	-	-	-	-	-	1	1	1	-	-	-	-	-
21	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
22	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
23	-	-	1	-	-	-	1	1	1	-	-	1	-	-	1	1	-	-	-
24	-	1	-	1	-	-	1	-	-	-	-	-	-	2	-	-	-	-	-

TLQ No.	Mar. 2	Mar. 9	May 4,6	May 11	May 19	May 26	June 3	June 9	June 17	June 24	July 1	July 7	July 14	July 21	July 28	Total	Square Meters of Unobscured Bottom	No. Individuals /m² Unobscured Bottom
1	-	-	1	-	-	1	1	2	1	-	-	-	-	-	-	26	33.00	0.788
2	-	1	1	1	3	-	-	-	1	1	1	1	-	-	-	21	34.10	0.616
3	1	-	1	-	-	-	1	1	-	-	1	-	2	-	-	22	42.46	0.518
4	-	-	-	-	-	2	3	-	1	-	1	2	1	1	-	24	47.62	0.504
5	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	3	48.04	0.062
6	-	-	-	1	-	-	-	-	-	1	-	1	-	-	-	14	38.24	0.366
7	1	-	1	-	-	-	-	2	3	2	-	1	-	-	-	23	42.04	0.547
8	1	2	1	1	1	1	2	-	-	3	1	3	1	4	-	59	50.86	1.160
9	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	17	50.95	0.334
10	1	1	-	-	-	-	1	-	-	-	-	-	-	-	1	19	51.00	0.373
11	-	-	1	2	-	2	1	-	-	-	-	-	1	-	-	13	50.96	0.255
12	-	-	2	1	1	1	-	1	-	-	1	1	-	2	-	20	50.88	0.393
13	-	-	1	1	1	1	1	-	-	-	-	-	-	-	1	10	50.97	0.196
14	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	15	50.88	0.295
15	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	8	50.77	0.156
16	1	2	-	-	1	1	-	-	-	-	-	-	-	1	-	15	51.00	0.294
17	-	-	-	-	-	-	1	1	-	1	-	1	-	-	-	14	50.96	0.275
18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	8	51.00	0.157
19	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	5	51.00	0.098
20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	51.00	0.118
21	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	4	51.00	0.078
22	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	3	51.00	0.059
23	-	-	-	1	-	-	-	-	-	-	-	1	-	1	-	10	51.00	0.196
24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	6	51.00	0.118

Appendix G. Number of observed individuals of Henricia eschrichti per TLQ for 35 sampling dates, including yearly mean number of individuals per square meter of unobscured bottom per TLQ.

TLQ No.	Jul. 30	Aug. 6	Aug. 13	Aug. 24	Sept. 3	Sept. 10	Sept. 15	Sept. 28	Oct. 5	Oct. 15	Oct. 20	Nov. 2	Nov. 9	Nov. 23	Dec. 3	Dec. 17	Jan. 12	Feb. 2	Feb. 9
1	-	-	-	-	-	-	-	1	1	-	2	1	3	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	2	2	-	1	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
5	-	-	1	-	-	1	-	1	-	-	-	-	1	-	-	-	-	-	-
6	-	-	2	-	-	-	-	-	-	-	-	1	1	1	-	2	-	1	-
7	-	-	3	-	1	-	2	3	4	1	1	-	5	1	1	4	-	1	-
8	2	3	2	2	3	3	-	5	2	2	3	3	6	2	1	2	3	4	1
9	-	2	2	1	3	2	-	1	-	1	3	1	2	-	2	-	-	1	-
10	1	1	3	-	-	1	1	1	2	-	1	-	1	-	2	-	-	-	3
11	-	-	-	-	-	-	-	2	1	-	-	2	2	2	1	1	-	2	-
12	-	-	3	1	-	1	-	-	-	1	2	-	1	1	-	-	-	-	-
13	-	-	-	-	-	1	-	1	1	1	1	-	-	-	-	-	1	-	-
14	1	1	4	1	1	3	-	-	1	1	-	-	-	-	-	-	-	-	-
15	-	-	2	-	-	-	-	1	1	-	-	-	1	4	-	-	2	-	-
16	-	1	2	1	-	-	1	-	1	1	2	-	2	1	2	1	4	-	2
17	-	-	4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-
18	-	-	2	-	-	1	1	-	-	-	-	1	-	1	1	2	1	1	1
19	1	1	6	1	-	4	3	-	2	3	2	2	2	2	2	-	-	3	-
20	-	1	6	-	-	2	3	2	4	1	1	5	5	1	2	-	2	4	2
21	1	-	1	2	3	2	-	1	2	3	2	1	4	2	2	1	2	1	3
22	1	3	5	4	3	5	2	2	4	3	-	-	3	3	-	-	2	1	4
23	-	1	3	1	1	2	3	1	1	1	1	2	-	-	-	-	1	-	-
24	-	1	2	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-

TLQ No.	Mar. 2	Mar. 9	May 4,6	May 11	May 19	May 26	June 3	June 9	June 17	June 24	July 1	July 7	July 14	July 21	July 28	Total	Square Meters of Unobscured Bottom	No. of Individuals /m^2 Unobscured Bottom
1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	10	33.00	0.303
2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	6	34.10	0.176
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	42.46	0.047
4	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	4	47.62	0.084
5	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	6	48.04	0.125
6	1	1	-	-	-	-	-	-	-	-	1	2	-	2	1	17	38.24	0.445
7	-	1	-	2	-	2	-	1	3	1	1	1	-	1	-	37	42.04	0.880
8	-	1	-	-	-	-	1	1	1	1	1	5	1	1	-	62	50.86	1.219
9	-	-	1	1	-	-	1	-	-	-	1	1	-	1	-	27	50.95	0.530
10	-	1	-	1	-	-	2	2	1	1	-	1	-	2	-	28	51.00	0.549
11	2	1	-	2	-	-	-	-	2	1	1	-	-	1	1	24	50.96	0.471
12	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	12	50.88	0.236
13	-	-	-	1	-	1	-	-	-	1	-	-	-	1	1	11	50.97	0.216
14	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	14	50.88	0.275
15	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	12	50.77	0.236
16	-	2	1	-	1	-	-	-	-	-	-	-	-	-	-	25	51.00	0.490
17	1	1	1	-	-	-	1	-	-	-	1	-	1	1	-	13	50.96	0.255
18	-	1	1	-	-	-	-	-	-	1	-	-	1	-	-	16	51.00	0.314
19	-	2	1	3	-	-	-	-	-	1	-	-	-	-	-	41	51.00	0.804
20	1	1	2	2	1	-	-	-	-	1	2	4	3	8	5	71	51.00	1.392
21	2	7	3	6	3	5	3	2	2	2	1	3	3	2	2	79	51.00	1.549
22	3	3	4	7	4	4	1	6	4	6	5	2	3	5	2	104	51.00	2.039
23	1	3	2	1	1	2	2	1	2	2	1	-	-	-	-	36	51.00	0.706
24	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	7	51.00	0.137

Appendix H. Number of observed individuals of Crossaster papposus per TLQ for 35 sampling dates, including yearly mean number of individuals per square meter of unobscured bottom per TLQ.

TLQ No.	Jul. 30	Aug. 6	Aug. 13	Aug. 24	Sept. 3	Sept. 10	Sept. 15	Sept. 28	Oct. 5	Oct. 15	Oct. 20	Nov. 2	Nov. 9	Nov. 23	Dec. 3	Dec. 17	Jan. 12	Feb. 2	Feb. 9
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	-	1	1	-	-	-	-	-	-	1	2	1	1	2	2	2	1	1	1
12	-	-	1	-	-	-	1	1	1	-	1	1	-	2	1	-	3	2	1
13	1	1	1	1	1	1	-	-	-	1	-	-	-	-	-	1	-	-	-
14	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	1	1	1	-	-	-	-	-	1	1	-	1	1	-	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
17	-	1	-	1	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
18	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
21	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
22	1	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1	-
23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TLQ No.	Mar. 2	Mar. 9	May 4,6	May 11	May 19	May 26	June 3	June 9	June 17	June 24	July 1	July 7	July 14	July 21	July 28	Total	Square Meters of Unobscured Bottom	No. Indiviuals /m² Unobscured Bottom
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	33.00	0.000
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	34.10	0.000
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	42.46	0.000
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	47.62	0.000
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	48.04	0.000
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	38.24	0.000
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	42.04	0.000
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	50.86	0.000
9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	50.95	0.000
10	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	51.00	0.039
11	1	-	-	-	-	-	-	1	-	-	-	-	-	1	-	19	50.96	0.373
12	-	1	-	-	-	-	-	-	-	1	-	-	-	-	1	18	50.88	0.354
13	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	10	50.97	0.196
14	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	6	50.88	0.118
15	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	8	50.77	0.158
16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	51.00	0.039
17	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	5	50.96	0.098
18	-	1	1	1	1	-	-	-	-	1	-	-	-	-	-	8	51.00	0.156
19	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	51.00	0.020
20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	51.00	0.020
21	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	3	51.00	0.059
22	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	7	51.00	0.137
23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	51.00	0.000
24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	51.00	0.020

Appendix I. Mean number of individuals of Solaster endeca, Henricia sp., and Leptasterias polaris (≤ 1.25 cm) per square meter of unobscured bottom.

TLQ No.	Solaster endeca	Henricia sp.	Leptasterias polaris (≤ 1.25 cm)
1	0	0	0.121
2	0	0	0.088
3	0	0	0.024
4	0	0	0.021
5	0	0	0.021
6	0	0	0
7	0	0	0.262
8	0	0	0.138
9	0	0	0.098
10	0	0	0.059
11	0	0	0.059
12	0	0	0.020
13	0	0.060	0.020
14	0	0	0
15	0	0	0
16	0	0	0.020
17	0	0.029	0.059
18	0	0.060	0.039
19	0.029	0.088	0.059
20	0.059	0	0.078
21	0.029	0	0.078
22	0	0	0.020
23	0.059	0	0.039
24	0	0	0

Appendix I (cont'd) Mean number of individuals of Asterias vulgaris ($\leq$ 1.25 cm), and unidentified asteroids ($\leq$ 1.25 cm) per square meter of unobscured bottom.

TLQ No.	*Asterias vulgaris* (≤ 1.25 cm)	Unidentified Asteroids (≤ 1.25 cm)
1	0.121	0.515
2	0.147	0.762
3	0.047	0.377
4	0	0.168
5	0.042	0.229
6	0.052	0.288
7	0.167	1.308
8	0.118	1.140
9	0.039	0.569
10	0.118	0.765
11	0.098	0.549
12	0.118	0.275
13	0.039	0.275
14	0.020	0.334
15	0.059	0.295
16	0.020	0.471
17	0.020	0.334
18	0	0.549
19	0.078	0.529
20	0.078	0.392
21	0.098	0.608
22	0.059	0.647
23	0.118	0.471
24	0	0.118

Appendix J. Relative abundance (percentage), based on yearly mean abundances, of Leptasterias polaris (≥ 1.5 cm), Asterias vulgaris (≥ 1.5 cm), Henricia eschrichti, Crossaster papposus, Henricia sp., and Solaster endeca.

TLQ No.	Leptasterias polaris	Asterias vulgaris	Henricia eschrichti	Crossaster papposus	Henricia sp.	Solaster endeca
1	69.745	21.852	8.403	-	-	-
2	67.461	25.308	7.231	-	-	-
3	74.481	23.397	2.123	-	-	-
4	71.717	24.242	4.040	-	-	-
5	87.348	4.195	8.457	-	-	-
6	41.486	26.407	32.107	-	-	-
7	44.453	21.292	34.255	-	-	-
8	42.383	28.094	29.523	-	-	-
9	54.622	17.542	27.836	-	-	-
10	47.194	21.363	31.443	-	-	-
11	44.551	12.866	23.764	18.819	-	-
12	43.179	22.717	13.642	20.462	-	-
13	49.255	15.373	16.941	15.373	3.059	-
14	48.542	22.064	20.568	8.826	-	-
15	38.227	17.238	26.077	17.459	-	-
16	39.127	21.746	36.243	2.885	-	-
17	49.216	21.552	19.984	7.680	1.567	-
18	40.376	14.056	28.111	13.966	3.491	-
19	32.864	6.573	53.924	1.344	3.957	1.344
20	30.421	5.234	61.729	0.887	-	1.729
21	17.941	3.752	74.507	2.838	-	0.962
22	15.565	2.229	77.031	5.176	-	-
23	26.865	14.916	53.729	-	-	4.490
24	56.210	18.790	21.815	3.185	-	-
Total R.A.	47.710	17.691	29.970	3.974	0.349	0.307

Appendix K. Mean number of individuals of Leptasterias polaris (≥1.5 cm) per square meter of unobscured bottom for four TLQ blocks for 35 sampling dates.

Appendix L. Mean number of individuals of Asterias vulgaris (≥ 1.5 cm) per square meter of unobscured bottom for four TLQ blocks for 35 sampling dates.

Appendix M. Mean number of individuals of Henricia eschrichti per square meter of unobscured bottom for four TLQ blocks for 35 sampling dates.

Appendix K

TLQ Block	July 30	Aug. 6	Aug. 13	Aug. 24	Sept. 3	Sept. 10	Sept. 15	Sept. 28	Oct. 6	Oct. 15	Oct. 20	Nov. 2	Nov. 9	Nov. 23	Dec. 3	Dec. 17	Jan. 12	Jan. 26	Feb. 2	Feb. 9
1 - 6	0.543	0.500	0.915	3.017	1.419	1.933	1.731	2.436	2.074	2.733	1.477	1.810	1.261	3.047	2.144	2.034	1.020	2.517	0.334	2.032
7 - 12	0.637	0.873	1.420	1.942	1.155	0.803	1.620	1.353	2.245	1.782	1.002	0.667	1.002	1.224	1.561	1.226	1.338	0.680	0.780	1.003
13 - 18	0.444	0.222	0.444	0.557	0.697	0.444	0.333	0.556	0.667	0.556	0.444	1.556	0.778	0.555	0.444	0.888	0.556	0.000	0.889	0.889
19 - 24	0.556	0.667	1.111	0.556	0.566	0.111	0.222	0.222	0.222	0.333	0.667	0.444	0.333	0.667	0.444	0.556	0.555	0.000	0.444	0.556

Appendix L

1 - 6	0.362	1.000	0.152	0.452	0.258	0.387	0.494	0.464	0.461	0.456	0.909	0.452	0.688	0.112	0.564	0.904	0.340	0.168	0.000	0.903
7 - 12	0.128	0.375	0.473	0.364	0.000	0.688	1.157	0.338	1.122	0.223	0.780	0.455	1.225	0.556	1.115	0.557	0.780	0.000	0.334	0.334
13 - 18	0.444	0.222	0.333	0.111	0.232	0.000	0.111	0.444	0.444	0.556	0.111	1.000	0.111	0.111	0.444	0.333	0.000	0.000	0.000	0.222
19 - 24	0.000	0.111	0.333	0.111	0.333	0.111	0.333	0.111	0.111	0.000	0.000	0.222	0.111	0.444	0.111	0.111	0.222	0.000	0.000	0.000

Appendix M

1 - 6	0.000	0.000	0.457	0.000	0.129	0.000	0.000	0.232	0.115	0.228	0.568	0.339	0.688	0.113	0.000	0.226	0.000	0.336	0.334	0.000
7 - 12	0.383	0.749	1.538	0.485	0.808	0.803	0.347	1.353	1.010	0.557	1.114	0.667	1.893	0.667	0.778	0.778	0.334	0.680	1.003	0.446
13 - 18	0.111	0.222	1.556	0.223	0.116	0.556	0.222	0.222	0.444	0.444	0.333	0.111	0.333	0.667	0.333	0.333	0.889	0.000	0.222	0.333
19 - 24	0.333	0.778	2.556	0.889	0.778	1.667	1.222	0.778	1.444	1.222	0.667	1.111	1.667	0.889	0.667	0.111	0.778	0.000	1.000	1.000

Appendix K

TLQ Block	Mar. 2	Mar. 9	May 4,6	May 11	May 19	May 26	June 3	June 9	June 17	June 24	July 1	July 7	July 14	July 21	July 28
1 - 6	0.569	1.477	1.056	0.771	0.478	0.780	0.720	0.877	1.153	1.381	1.237	1.048	1.464	1.131	1.167
7 - 12	0.669	1.568	0.894	1.116	1.121	0.451	0.571	0.466	1.136	1.296	0.238	0.503	0.616	0.770	0.930
13 - 18	0.667	0.667	0.333	0.222	0.444	0.667	0.333	0.333	0.667	0.444	0.222	0.333	0.333	0.222	0.889
19 - 24	0.889	0.333	0.556	0.556	0.111	0.111	0.333	0.222	0.111	0.333	0.333	0.889	0.333	0.556	0.222

Appendix L

1 - 6	0.114	0.114	0.470	0.237	0.358	0.520	0.720	0.439	0.494	0.394	0.618	0.839	0.627	0.226	0.000
7 - 12	0.334	0.448	0.559	0.446	0.224	0.451	0.571	0.350	0.341	0.589	0.238	0.629	0.246	0.770	0.116
13 - 18	0.111	0.222	0.111	0.222	0.444	0.222	0.333	0.222	0.111	0.111	0.000	0.111	0.000	0.111	0.222
19 - 24	0.000	0.000	0.000	0.222	0.000	0.111	0.111	0.000	0.000	0.111	0.000	0.111	0.000	0.111	0.222

Appendix M

1 - 6	0.114	0.455	0.000	0.118	0.000	0.000	0.000	0.000	0.329	0.000	0.412	0.419	0.000	0.452	0.195
7 - 12	0.223	0.448	0.112	0.670	0.112	0.226	0.456	0.466	0.795	0.589	0.416	1.006	0.123	0.770	0.116
13 - 18	0.111	0.444	0.333	0.111	0.111	0.111	0.111	0.111	0.000	0.222	0.111	0.000	0.222	0.333	0.111
19 - 24	0.778	1.778	1.333	2.111	1.000	1.333	0.667	1.111	0.889	1.333	1.000	1.000	1.000	1.667	1.000